COLLECTED REPRINTS

1989

VOLUME I
A - N

NATIONAL MARINE FISHERIES SERVICE
SOUTHWEST FISHERIES SCIENCE CENTER

Library
NOAA, National Marine Fisheries Service
SWFC Honolulu Laboratory F/SWC2
2570 Dole Street
Honolulu, HI 96822-2396

Digitized by the Internet Archive
in 2025

https://archive.org/details/nmfs-swc-collected-reprints_1985_2_k-z

NATIONAL MARINE FISHERIES SERVICE
SOUTHWEST FISHERIES SCIENCE CENTER

COLLECTED REPRINTS

1989

VOLUME I

A: 8901
N: 8946

AUGUST 1993

TABLE OF CONTENTS

BAKUN, A. 1989. Mechanisms for density-dependent growth of anchoveta: alternatives to impact on the regional-scale food supply, pp. 235-243. *In* Pauly, D., P. Muck, J. Mendo, and I. Tsukayama (eds.). The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.. 8901

——————. 1989. Recruitment in fishery resources and its relationship to environment: accessible pathways to greater insight, pp. 25-34. *In* Memorias del Simposio International de los Recursos Vivos y las Pesquerías en el Pacífico Sudeste, Viña del Mar, May 9-13, 1988. Rev, Pacífico Sur (Número Especial). Comisión Permanente del Pacífico Sur (CPPS).. 8902

BAKUN, A., AND R. MENDELSSOHN. 1989. Alongshore wind stress 1953-84: correction, reconciliation and update through 1986, pp. 77-81. *In* Pauly, D., P. Muck, J. Mendo, and I. Tsukayama (eds.). The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.. 8903

BALAZS, G. H. 1989. New initiatives to study sea turtles in the eastern Pacific. Mar. Turtle Newsl. 47:19-21. 8904

BARTOO, N. W., AND A. L. COAN, JR. 1989. An assessment of the Pacific swordfish resource. *In* Stroud, R. H. (ed.), Planning the future of billfishes. Part 1: Fishery and stock synopses, data needs and management. Mar. Rec. Fish. 13:137-151. Natl. Coalition Mar. Conserv., Savannah, GA. 8905

BERNARD, H. J., AND A. A. HOHN. 1989. Differences in feeding habitats between pregnant and lactating spotted dolphins (*Stenella attenuata*). J. Mammal. 70(1):211-215. 8906

BOEHLERT, G. W. 1989. Drift net problems spread to South Pacific. Hawaii Fish. News 13(12):34. 8907

TABLE OF CONTENTS (CONTINUED)

HOLT, R. S., AND S. N. SEXTON. 1989. Monitoring trends in dolphin abundance in the eastern tropical Pacific using research vessels over a long sampling period: analyses of 1987 data. Rep. int. Whal. Commn 39:347-351. 8928

HUMPHREYS, R. L., JR., R. B. MOFFITT, AND M. P. SEKI. 1989. First record of the bigeye sand tiger shark *Odontaspis noronhai* from the Pacific Ocean. Jpn. J. Ichthyol. 36(3):357-362. 8929

HUMPHREYS, R. L., JR., G. A. WINANS, AND D. T. TAGAMI. 1989. Synonymy and life history of the North Pacific pelagic armorhead, *Pseudopentaceros wheeleri* Hardy (Pisces: Pentacerotidae). Copeia 1989(1):142-153. 8930

HUNTER, J. R., B. J. MACEWICZ, AND C. A. KIMBRELL. 1989. Fecundity and other aspects of the reproduction of sablefish, *Anoplopoma fimbria*, in central California waters. Calif. Coop. Oceanic Fish. Invest. Rep. 30:61-72. 8931

JOKIEL, P. L. 1989. Effects of marine mining dredge spoils on eggs and larvae of a commercially important species of fish, the mahimahi (*Coryphaena hippurus*). Mar. Min. 8:303-315. 8932

LAPOINTE, M. R., R. M. PETERMAN, AND A. MACCALL. 1989. Trends in fishing mortality rate along with errors in natural mortality rate can cause spurious time trends in fish stock abundances estimated by virtual population analysis (VPA). Can J. Fish. Aquat. Sci. 46(12):2129-2139. 8933

LAURS, R. M. 1989. Applications of satellite remote sensing to North Pacific albacore, *Thunnus alalunga* (Bonnaterre). FAO Fisheries Technical Paper 302:87-97 (in French). 8934

——————. 1989. Review of satellite applications to fisheries. Proc. International Geoscience and Remote Sensing Symposium 1989 4:2037-2040.. 8935

LEONG, R. J. H. 1989. Sperm concentrations and egg fertilization rates during spawning of captive anchovy, *Engraulis mordax*. Calif. Coop. Oceanic Fish. Invest. Rep. 30:136-139. 8936

LLUCH-BELDA, R. J., M CRAWFORD, T. KAWASAKI, A. D. MACCALL, R. H. PARRISH, R. A. SCHWARTZLOSE, AND P. E. SMITH. 1989. World-wide fluctuations of sardine and anchovy stocks: the regime problem. S. Afr. J. Mar. Sci. 8:195-205. 8937

TABLE OF CONTENTS (CONTINUED)

LO, N. C. H., J. R. HUNTER, AND R. P. HEWITT. 1989. Precision and bias of estimates of larval mortality. Fish. Bull., U.S. 87(3):399-416. 8938

LO, N. C. H., AND R. D. METHOT. 1989. Spawning biomass of the northern anchovy in 1988. Calif. Coop. Oceanic Fish. Invest. Rep. 30:18-31. 8939

MACCALL, A. D. 1989. Against marine fish hatcheries: ironies of fishery politics in the technological era. Calif. Coop. Oceanic Fish. Invest. Rep. 30:46-48. 8940

MASON, J. E. 1989. The southern California jack mackerel fishery, and the age and length composition of the catch for the 1972-73 through 1983-84 seasons. Calif. Dep. Fish and Game, Mar. Res. Tech. Rep. 58, 38 p. 8941

MENDELSSOHN, R. 1989. A reanalysis of estimates of recruitment of the Peruvian anchoveta in relationship to the other population parameters and to the surrounding environment, pp. 364-385. *In* Pauly, D., P. Muck, J. Mendo, and I. Tsukayama (eds.). The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines. 8942

MENDELSSOHN, R., AND P. CURY. 1989. Temporal and spatial dynamics of a coastal pelagic species, *Sardinella maderensis*, off the Ivory Coast. Can. J. Fish. Aquat. Sci. 46(10):1686-1697. 8943

METHOT, R. D. 1989. Synthetic estimates of historical abundance and mortality for northern anchovy, pp. 66-82. *In* Edwards, E. F., and B. A. Megrey (eds.) Mathematical analysis of fish stock dynamics. Am. Fish. Soc. Symp. 6. 8944

MOFFITT, R. B., F. A. PARRISH, AND J. J. POLOVINA. 1989. Community structure, biomass and productivity of deepwater artificial reefs in Hawaii. Bull. Mar. Sci. 44(2):616-630.. 8945

NELSON, D. M., W. O. SMITH, JR., R. D. MUENCH, L. I. GORDON, C. W. SULLIVAN, AND D. M. HUSBY. 1989. Particulate matter and nutrient distribution in the ice-edge zone of the Weddell Sea: relationship to hydrography during late summer. Deep-Sea Res. 36(2):191-209.. 8946

8901

Mechanisms for Density-Dependent Growth in Peruvian Anchoveta: Alternatives to Impact on the Regional-Scale Food Supply

ANDREW BAKUN
Pacific Fisheries Environmental Group
Southwest Fisheries Center
National Marine Fisheries Service, NOAA
P.O. Box 831, Monterey
California 93942, USA

KUN, A. 1989. Mechanisms for density-dependent growth in Peruvian anchoveta: alternatives to impact on the regional-scale food supply, p. 235-243. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Abstract

Two alternate classes of mechanisms that could account for evidence of density-dependent growth are introduced: (i) effects of potential kages of school size with population size, and (ii) effects of size-dependent predation. These may lead to different interpretations with respect resilience to exploitation, carrying capacity of the habitat, etc., from those implied by the more commonly cited class of mechanisms which volve impact of the population on its food supply.

Resumen

Dos mecanismos alternos que evidenciarían la denso-dependencia del crecimiento son introducidos: (i) efectos de relaciones potenciales el tamaño del cardumen con el tamaño de la población y (ii) efectos de la dependencia del tamaño con la predación. Estos pueden conducir a iferentes interpretaciones con respecto a la repercusión para la explotación, capacidad de carga del habitat, etc., de aquellas implicadas por las lases de mecanismos más comunmente citadas que abarcan el impacto de la población sobre su suministro de alimento.

Introduction

An apparent dependence of growth on population density is a common finding in studies of the dynamics of natural fish populations (e.g., Beverton and Holt 1957; Ware 1980). The mechanism commonly proposed involves increased competition for available food at high population density.

In the case of small coastal pelagic fish such as anchovies and sardines inhabiting coastal upwelling systems, the extent to which this type of mechanism might really be acting is not clear. For example, Lasker (1970) estimated that at peak population size, the Pacific sardine would have consumed more than the entire secondary production in California's current ecosystems. Nevertheless, no growth increase was noted among adults as the population declined (Murphy 1973). In the similar eastern ocean boundary upwelling ecosystem off Northwest Africa, Mathisen et al. (1978) compared food consumption to food production. Results suggested that food does not directly control the size of adult or recruited fish populations. Mathisen et al. cited Gulland (1971), Murphy (1973) and Steele (1974) as having questioned food limitation as a control for adult fish "since in those cases where fish have been reduced to a low level through fishing, the structure and size of the next lower trophic level has not changed drastically". In the case of the Peru Current upwelling system, Lasker (1989) estimates that the anchoveta population, at a pre-collapse biomass level of 20 million t, would consume about one-fourth of the primary production of the ecosystem (note that the value "40", rather than "4", in Lasker's published paper is apparently a typographical error). Since anchoveta obviously will consume some quantity of secondary production, the question as to whether it may at times be limited by its food supply is unanswered.

Indeed, Palomares et al. (1987) found a significant correlation between growth performance and population biomass of Peruvian anchoveta over the period 1954-1982. They discussed three different effects which might have increased growth rates as the population declined: (1) decreased competition for available food due to fewer competing individuals, (2) a relative increase in abundance of more nutritious zooplankton, due to lessened competition for food resources and lessened predation by anchoveta, *vis à vis* less nutritious phytoplankton, and (3) a corresponding increased proportion of more efficient particulate feeding on zooplankton relative to less efficient filter feeding on phytoplankton. All three effects fall under the class of mechanisms implying a substantial impact of feeding activity on the amount or composition of the regional-scale food supply. Since natural mortality is generally size-dependent, and therefore growth-dependent, such a directly-linked impact of the population on its own food supply would seem to constitute a powerful compensatory mechanism with respect to effects of fisheries exploitation.

The purpose of this chapter is to point out that plausible alternative mechanisms exist which do not necessarily imply a substantial impact on the large-scale food supply. Two classes of mechanisms will be addressed: (1) effects of school size, and (2) effects of size-dependent predation. These may lead to different interpretations of evidence of density-dependent growth with respect to resilience of the population to exploitation, potential carrying capacity of habitat, etc.

Effects of School Size

Consequences of Fish School Geometry

As fish schools vary in diameter, they may also vary correspondingly in vertical thickness, i.e., large schools may be thicker in vertical dimension than small schools. To the extent that school thickness may vary in rough proportion to school diameter, the areal aspects of the school geometry, such as the surface area encompassing the volume occupied by the school or the cross-sectional area swept by school movement, will vary as the second power of δ (where δ = school diameter or other appropriate characteristic length scale). However, the volume of the school, and therefore, the number of individual fish contained, will vary as the third power of δ. Thus,

$$\frac{\text{school surface area}}{\text{school volume}} \propto \frac{\text{cross-sectional area swept}}{\text{no. of individuals in school}} \propto \frac{1}{\delta} \qquad \text{...1)}$$

The consequence of expression (1) is that as δ (i.e., school size) increases, the average supply per individual within the school of food and other substances (e.g., replenished dissolved oxygen where concentration may have been depleted by respiration) that must enter the school interior through the cross-sectional area swept by a moving school (or diffused through the outer surface area of a stationary school) decreases in proportion to δ^{-1}. Thus, a fish in a larger school (of size ~ δ_1) must, in comparison to a fish in a smaller school (of size ~ δ_2), either accept an average food ration which is smaller by the factor δ_2/δ_1 (and to the extent that a school may be capable of depleting the oxygen within the water volume occupied, the additional detriment of a lowered uptake rate of oxygen) or carry the metabolic costs of swimming faster by a factor of

δ_1/δ_2. Kils (1979) discussed this effect as a factor limiting the school size of the Antarctic krill *Euphausia superba*.

Of course, it is possible that large schools are strictly limited in the vertical dimension by external constraints (water column structure, total water depth in shallow areas, vertical distribution of food organisms, etc.). In the case of a flattened school shape of constant vertical dimension, the volume and the surface area of a school vary nearly in direct proportion. Even so, the ratio of cross sectional area swept to the volume of a moving school would continue to vary as δ^{-1} so long as both horizontal dimensions tend to increase or decrease together (i.e., excluding the case where the length of the school axis parallel to its motion remains constant while school width, normal to the direction of motion, increases.) Actually, Mais (1974) finds seasonal, diurnal, and other (e.g., relation to topography) tendencies for school sizes and for school thicknesses to vary somewhat in phase, such that thicknesses of larger schools of northern anchovy off California tend to be greater than those of smaller schools. However, one finds little information in the literature on school thickness in relation to school diameter; this may indicate a lack of appreciation of the potential importance of school surface to volume ratios with respect to nutrition and metabolism of schooling fish.

Should Average School Size Increase with Population Size?

Pitcher (1986) cites potential advantages of schooling behavior in fish including hydrodynamic advantages, countering predation, discovery of food patches, and opportunities for group learning. In any case, it seems clear that for species with pronounced schooling behavior, individuals or small groups of fish must tend to increase their probability of survival and successful propagation of their genetic material by joining with other conspecific groups of similar body size that might be encountered. Thus, in the absence of processes tending to fragment the school, school size would tend to increase with time. The expected rate of increase depends on the rate of encounter with other individuals or schools; that is, all other factors being equal, it should be roughly proportional to population density, i.e.,

$$\text{number of individuals joining a given school per unit time} \quad \propto \quad P^c \qquad \ldots 2)$$

where P is the size of the population, and the exponent c ($0<c\leq 1$) represents MacCall's (1980) suggestion for incorporation of variable habitat size in representing a density-dependent mechanism (i.e., $c = 0$ implies that habitat size varies in proportion to population size and thus, that population density does not vary with population size; $c = 1$ implies that there is no habitat size variation and thus, that population density varies directly with population size; $0<c<1$ implies the less-than-proportional increase of habitat size with population size which, for coastal pelagic fish populations, appears to fit observations).

Obviously, processes tending to fragment schools become substantial at some point or the entire population would tend to aggregate into a few very large schools, whereas large numbers of disjoint schools is the observed situation. This implies that, while the tendency for aggregation must dominate when the school size is small, processes of fragmentation must become increasingly important as school size increases, i.e.,

$$\text{number of individuals leaving a given school per unit time} \quad = \quad F(N) \qquad \ldots 3)$$

where F(N) is some increasing function of N (N = number of individuals in a school), at least over an observed range of school sizes. Combining expressions (2) and (3) yields

$$\frac{dN}{dt} = kP^c - F(N) \qquad \ldots 4)$$

where k is the constant of proportionality implied by expression (2). Using a formulation equivalent to equation (4), Anderson (1981) added the assumptions that the number leaving was linearly proportional to N (i.e., $F(N) = K N$, where K is a constant) and that the number joining (kP^c) was constant with time. He added stochastic terms to the entrance and exit rates and to the relationship of N to δ. He thereby constructed a model that reproduced the frequency distribution of pelagic fish school diameters off Southern California reported by Smith (1970).

The question of the form of F(N) is an important one. There must be some ultimate limiting point at which the school size becomes too large for its members to meet their metabolic requirements. Upon growing to that point, it would seem that the school must become unstable and break apart. However, Smith (1981) reports a substantial range of school sizes of coastal pelagic fish rather than the tight modal distribution that would suggest that school size is controlled only by the ultimate metabolic limit. Apparently, other processes of fragmentation act over a range of sizes well below that point.

The hypothesis that individuals altruistically leave the school when they perceive that it is becoming too large for peak efficiency appears to be untenable. A principle of behavioral ecology states that animals do not sacrifice their own fitness for the good of their group (e.g., Grafen 1984). Various models (Sibly 1983; Pulliam and Caraco 1984; Clark and Mangel 1984) indicate that the optimum group size is unstable and that group sizes in natural systems are considerably larger than optimal size. This is because individuals do better in a group (even an oversized group), than on their own. Pitcher (1986) draws the analogy to an overcapitalized fishery in which individuals will not withdraw in order to increase the profit of those remaining in the fishery as long as they themselves have not reached the point of zero profit. The effect of natural selection is to ensure that individual fish within a school maximize the probability of successfully propagating their own genetic material relative to that of other individuals in the school. Natural selection would thus act to obliterate this type of altruistic behavior.

Having rejected the hypothesis that altruistic behavior by individuals provides the mechanism for removing fish from a school, it is difficult to envision behavioral responses that would induce other individuals to exit the school while allowing the initiators to stay. The remaining possibilities include stochastic effects such as amplified random motions within a school that might lead to polarized movements in different directions by different segments of a school such that fish in between must relinquish their attraction to one of the segments to stay with the other. The two segments could thereby lose contact, thus splitting the school into two smaller schools. A related effect might occur when two separate food patches are encountered at two sides of the moving school front. Feeding behavior would attract school members to one or the other of the food patches, leading to a similar loss of contact between school segments (Paul E. Smith, pers. comm.). Also, it is possible that predator attack could fragment a school, although Pitcher (1986) emphasizes that the observed tendency under attack is for increased school cohesiveness.

In these cases, the average number of fish leaving a school per unit time should, on average, be proportional to the total number in the school at the time a fragmentation occurs; i.e., $F(N) = K N$ (where K is a constant of proportionality), as assumed by Anderson (1981). With this substitution, the equilibrium solution to equation (4) is $kP^c = K N$, or

$$\text{equilibrium school size} \equiv \tilde{N} = \left(\frac{k}{K}\right) P^c \qquad \text{...5)}$$

Equation (5) predicts that average school size will increase with population size provided $c \neq 0$ (i.e., provided population density increases with population size.) In fact, even if k and K are not constants, the two premises: (i) that the rate of entry into a school increases with population size, and (ii) that the rate of leaving the school increases with school size, must lead to an equilibrium that shifts to larger school sizes as population size increases. Of course, the actual distribution of school sizes might reflect large, possibly highly nonsymmetrical, stochastic variability about such an equilibrium.

Mais (1974) found that the discrete daytime schools of northern anchovies off California tended to break up into scattering layers at night. This is in accord with the common pattern for clupeoids (Blaxter and Hunter 1982). This particular type of shift in school size and character does not necessarily imply altruism by individuals, but merely an alteration in attraction and cohesion due to changes in visual acuity with the drastic day-night change in light. Different values of k and F(N) in equation (4) resulting from the changed attractive and cohesive properties would lead to two different effective equilibrium school sizes depending on day or night conditions. Mais also found that the distribution of school sizes is somewhat dependent on season. Seasonal changes in behavior, food patch size spectra, etc. could result to variations in attraction to the school (i.e., in k) or in cohesiveness (i.e., in F(N)) leading to seasonal variation in $\tilde{N}$. He also noted extremely large dense schools forming along steep bottom gradients of submarine canyons or escarpments. In this case, the topographic features could in themselves attract fish (i.e., act to effectively increase k on a very local scale) and provide points of orientation which could counteract the tendency for school fragmentation as a result of random motions of polarized school segments (thereby decreasing F(N)). The result would be a corresponding local increase in $\tilde{N}$. In all of these cases, equation (4) could separately apply to each diurnal, seasonal, or local situation, with the net integrated result that average school size in the habitat would increase with population size.

Applicability to the Anchoveta

Jordan (1971) notes that anchoveta form large, dense schools during the daylight hours which break up at night into smaller feeding schools. This may be a simplification of a more complex situation similar to that described by Mais (1974) for the northern anchovy. However, it will be useful to discuss the problem on this basis. In that case, the considerations presented above could act on both scales: (i) in the formation of the large daytime schools from a background "population" of feeding schools, and (ii) in the determination of the size distribution of nighttime feeding schools from the background population of individuals. In both cases, the effective value of P in equation (4) could depend on the total population size and the considerations presented above could thereby hold.

In the case of food ration, the nighttime case seems to be the pertinent situation to consider. In the smaller "feeding schools", a proportional variation of vertical dimension with horizontal dimension is most likely. In a tank experiment wherein relatively large food particles induced the "particulate" (i.e., "biting") feeding response, Leong and O'Connell (1969) found that a 64-fish school of northern anchovies received substantially less ration per unit time at a given particle density than did schools of 16 fish and less. J.R. Hunter (pers. comm.) has observed that anchovies in smaller schools tend to be less polarized in their behavior and more apt to make excursions from the main school trajectory in order to take particles lying outside of the school's main path; in larger schools, the individuals seem more controlled by cohesive behavior and therefore, apt to get less ration per individual.

In the case of oxygen supply, the large densely-packed daytime resting schools may constitute a situation where effects on oxygen uptake affect the ability to metabolize, and thereby utilize for growth, food taken during the feeding period (Pauly 1981). This writer is aware of no measurements of oxygen depletion taken at sea within a school of clupeoids. However, McFarland and Moss (1967) measured oxygen depletion within schools of striped mullet (*Mugil cephalus*). They found a reduction of dissolved oxygen within all schools measured. The magnitude of the reduction correlated with school size, ranging up to 29% (in a school of size $\delta = 150$ m). Actual values of the reduction were in the range of 0.12-0.40 mg L^{-1} for "small" ($\delta =$ 4-9 m) schools, 0.50-0.80 mg L^{-1} for "medium" ($\delta =$ 18-30 m) schools, and 0.70-2.10 mg L^{-1} for "large" ($\delta =$ 75-300 m) schools. Typical separation between fish within daytime anchoveta schools is of the order of one fish length (Jordan 1971) and so comparable reductions in dissolved oxygen concentration seem possible for large anchoveta schools. Brett (1979), in experiments with different fish species, found that a drop of dissolved oxygen of one mg L^{-1} causes a 30% reduction in growth rate.

Effect of Size-Dependent Predation

Small coastal pelagic fish such as anchovies attract a varied community of natural predators including sea birds, marine mammals and predatory fish. These predators tend to live longer than their smaller prey, and thus their population responses would tend to lag variations in their food supply. In many systems the predators have access to alternate prey. Switching of predation pressure to these alternate food resources is one likely response to population decline of a major prey species. But, because of the enormous size of the Peruvian anchoveta population prior to the 1971/72 collapse , and its corresponding dominance within the current Peru ecosystem, the opportunities for switching to alternative prey during the decline of the anchoveta might have been more limited than in more diversely populated ecosystems. Thus, predators without an option of migration to other feeding grounds, e.g., sea birds, marine mammals, etc., with strong local affinities, may have to attempt to derive continued sustenance by extracting an increased share of a declining food base.

On the other hand, predator populations that habitually migrate to exploit spatially separate food bases may not have to experience population declines due to decline in one of its major food bases. For example, Muck and Sanchez (1987) consider mackerel (*Scomber japonicus*) and horse mackerel (*Trachurus murphyi*) the most important predators of anchoveta throughout the entire era of high anchoveta biomass and the more recent era of lowered biomass. These fish exploit both the nearshore habitat of the anchoveta and the habitat further offshore. They are opportunistic feeders, shifting to zooplankton and euphasids where anchoveta are less available. In fact, Muck and Sanchez (1987) assume a constant biomass of mackerel and horse mackerel over the entire period of high anchoveta biomass and recent decline, and thereby infer a relative increase in specific predation rate in the recent period.

These considerations suggest a substantial increase in natural predation pressure on the anchoveta, per unit anchoveta biomass, since the decline. If, as suggested in the previous section, school size has also declined, this could further increase predation mortality (if one accepts the argument of Clark (1974)).

Predation mortality is thought to be size-dependent in both larval (Hunter 1971; Folkvord and Hunter 1986; Miller et al. 1988) and juvenile (Parker 1971; Healy 1982; Hargreaves and LeBrasseur 1986) fish. Thus, animals which grow quickly through the various vulnerable stages increase their chances of successful recruitment. Any larva or juvenile which by chance gets access to a better ration or other favorable growth condition thereby acquires an incrementally increased probability of avoiding predation. This effect cascades as the fish grow through the multitudinous series of size increments between hatching and recruitment, with the net result that slower-growing individuals make up a reduced portion of the survivorship as age increases. The mode of the distribution of size at age is shifted toward larger sizes (Fig. 1). Thus, the apparent growth rate computed from samples of survivors would be larger than the true growth rate, merely because of the biased mortality.

For example, Parker (1971) experimented on replicate populations of juvenile salmon in eight separate aquaria each having an identical, continually replenished food density. Thus, the true growth rates should have been identical. In half of the aquaria, three larger salmon were introduced as predators; the other half were kept predation-free as controls. After allowing time for the populations affected by predation to be substantially reduced, all the populations were measured. An increased growth rate of 0.3-0.5% per day was measured in the populations affected by predation, due entirely to the bias caused by size-dependent predation.

If, as suggested earlier, the relative predation pressure was indeed increased during the population decline of the anchoveta, this bias toward larger size at age and corresponding larger apparent growth rate would have been amplified. In such case, there is no need for alteration of actual growth rates to have occurred in order to produce the evidence of density-dependent growth in anchoveta reported by Palomares et al. (1987).

Discussion

Three classes of hypothetical mechanisms for density-dependent growth have been put forth for consideration:

1. Impact of the population variations on the ambient food supply,
2. Effects of linkages of school size with population size,
3. Effects of amplified size-dependent predation during population decline.

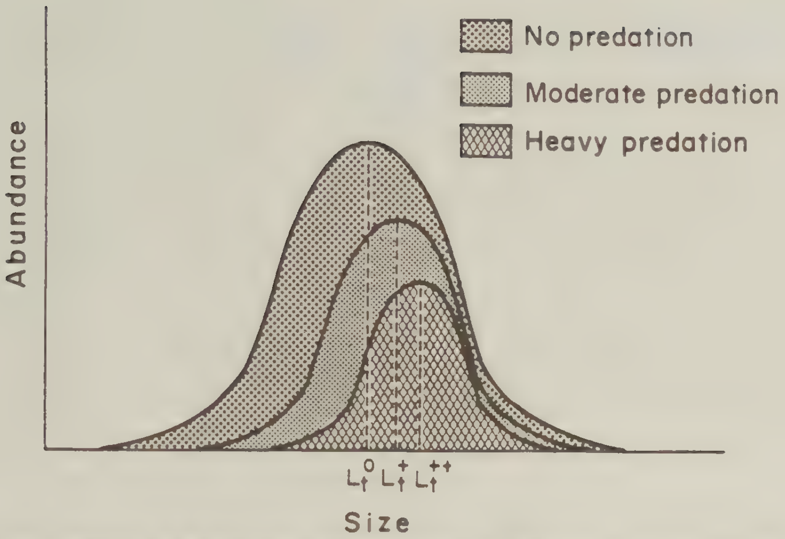


Fig. 1. Illustration of the apparent shift to larger size at age due to size-dependent predation. Where, if there had been no mortality due to predation the observed mean size at age "t" may have been L_t°, at a moderate level of predation it would be L_t^+. If predation mortality is increased, the abundance at age is lowered further, the distribution is shifted toward larger sizes and the observed size at age would be L_t^{++}. The result is: $L_t^\circ < L_t^+ < L_t^{++}$.

Fig. 1. Ilustración del cambio aparente a tamaños mayores en una edad debido a la predación dependiente tamaño. Donde, si no ha habido mortalidad debido a predación el tamaño promedio observado a una edad "t" puede haber sido L_t°*, a un nivel moderado de predación este sería* L_t^+*. Si la predación es incrementada, la abundancia a una edad es reducida además, la distribución es cambiada hacia mayores tamaños y el tamaño observado a esa edad sería* L_t^{++}*. El resultado es:* $L_t^\circ < L_t^+ < L_t^{++}$*.*

The first class is the one often considered. It has the comforting implication that, since the population would appear to be effectively eating up its food supply at high biomass, there must be substantial surplus production and associated compensatory resilience to exploitation. The second class of mechanisms also has compensatory implications, but does not imply, as does the first, that the population at high biomass may be nearing the limit of the carrying-capacity of its habitat. The third class of hypothetical mechanisms is not comforting at all, implying nothing but increased predation mortality during a population decline, i.e., a depensatory density-dependent process rather than a compensatory one.

In addressing the potential effect of school size, the relationship of vertical thickness to horizontal scale is a crucial aspect. To the extent that vertical and horizontal aspects may be functionally linked, important consequences of school size to nutrition, growth and metabolism are indicated. In fact, a general tendency toward vertically-flattened school shapes (Blaxter and Hunter 1982) may constitute an adaptation to avoid some of these consequences. Information on this functional linkage is surprisingly absent in the literature, although it would seem not difficult to acquire.

If there is a "moral" to this contribution, it illustrates the need for an "integrated ecosystem" view of marine resource population dynamics. We have seen the possibilities of three different interpretations of the same evidence, each with crucial, but highly differing, implications to stock management and preservation. To a fisheries oceanographer, the situation feels familiar. It is not very different from the dilemma faced in attempts to empirically sort out marine biological-environmental linkage mechanisms when one finds, in the typical case, that the available time series relating to various causal mechanisms are all highly intercorrelated and autocorrelated (e.g., Bakun 1987; Mendelssohn and Mendo 1987). The result is that available information is simply too limited to empirically differentiate among the possibilities.

How can we expect to make progress in sorting out the factors controlling marine resource population variability? Clearly, we need innovative approaches. And we need to recognize, integrate and utilize information on all the various scales, both spatial and temporal, that can be accessed. For example, this contribution indicates that in addressing issues of population ecology, it is important to consider processes occurring on the scale of the school (for that matter on perhaps two school scales, both of the nighttime "feeding" school and of the daytime "resting" school), as well as on the population habitat scale. To be blunt, fisheries science needs to expand beyond the "giant guppy tank" concept of an ecosystem, and relinquish the conventional "one-spatial/temporal aggregate-data-point-per-year" approach to variability, so as to be capable of utilizing all the information in the rich patterns of variation within years, and both within and among regions (Bakun, in press). The cooperative assembly and integrative analysis of various types of data reported in this volume and in the earlier companion volume (Pauly and Tsukayama 1987) can perhaps serve as a model in this direction, both in the attempt to address variability of higher than annual frequency, despite difficulties caused by interferences related to seasonal tuning of various processes, and in its making readily available the basic data for use by anyone with an innovative idea. If the concept were to be emulated in other regional systems, the comparative method of science (Mayr 1982) might constitute a potent tool for increasing the power of empirical analysis (Bakun 1985).

Acknowledgments

Discussions with John R. Hunter, Paul E. Smith, Gary D. Sharp and Richard H. Parrish have been extremely helpful in organizing my ideas for this contribution. However, any errors of naiveté or oversimplification are certainly my own.

References

Anderson, J.R. 1981. A stochastic model for the size of fish schools. U.S. Fish. Bull. 79: 315-323.

Bakun, A. 1985. Comparative studies and the recruitment problem: Searching for generalizations. CalCOFI Rep. 26: 30-40.

Bakun, A. 1987. Monthly variability in the ocean habitat of Peru as deduced from maritime observations, 1953-1984, p. 46-74. *In* D. Pauly, and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Bakun, A. Recruitment and its relationship to environment: accessible pathways to greater insight. *In* R. Jordan (ed.) Simposio Internacional Sobre Recursos Vivos y Pesquerías en el Pacifico Sudeste. Comisión Permanente de Pacifico Sur, Bogotá, Colombia. (In press)

Beverton, R.J.H. and S.J. Holt. 1957. On the dynamics of exploited fish populations. Fish. Invest. Ser. II. Vol. 19. 533 p.

Blaxter, J.H.S. and J.R. Hunter. 1982. The biology of the clupeid fishes. Adv. Mar. Biol. 20: 1-223.

Brett, J.R. 1979. Environmental factors and growth, p. 599-677. *In* W.S. Hoar, D.J. Randall, and J.R. Brett (eds.) Fish physiology. Vol. VIII. Bioenergetics and growth. Academic Press, New York.

Clark, C.W. 1974. Possible effects of schooling on the dynamics of exploited fish populations. J. Cons. CIEM 36: 7-14.

Clark, C.W. and M. Mangel. 1984. Foraging and flocking strategies: information in an uncertain environment. Am. Nat. 123: 626-641.

Folkvord, A. and J.R. Hunter. 1986. Size-specific vulnerability of northern anchovy (*Engraulis mordax*) larvae to predation by fishes. U.S. Fish. Bull. 84: 859-869.

Grafen, A. 1984. Natural selection, kin selection and group selection, p. 62-84. *In* J.R. Krebs and N.B. Davies (eds.) Behavioral ecology. Second edition, Blackwell, Oxford.

Gulland, J.A. 1971. Ecological aspects of fishery research. Adv. Ecol. Res. 7: 115-176.

Hargreaves, N.B. and R.J. LeBrasseur. 1986. Size-selectivity of coho (*Oncorhynchus kisutch*) preying on juvenile chum salmon (*O. keta*). Can. J. Fish. Aquat. Sci. 43: 581-586.

Healy, M. 1982. Timing and relative intensity of size-selective mortality of juvenile chum salmon (*Oncorhynchus keta*) during early sea life. Can J. Fish. Aquat. Sci. 39: 952-957.

Hunter, J.R. 1981. Feeding ecology and predation of marine fish larvae, p. 33-79. *In* R. Lasker (ed.) Marine fish larvae. Washington Sea Grant Program, University of Washington Press, Seattle.

Jordan, R. 1971. Distribution of anchoveta (*Engraulis ringens* J.) in relation to the environment. Inv. Pesq. 355(1): 113-126.

Kils, U. 1979. Performance of Antarctic krill *Euphausia superba*, at different levels of oxygen saturation. Meeresforsch. 27(1): 35-47.

Lasker, R. 1970. Utilization of zooplankton energy by a Pacific sardine population in the California current, p. 265-284. *In* J.H. Steele (ed.) Marine food chains. University of California Press, Berkeley.

Lasker, R. 1989. Food chains and fisheries: an assessment after 20 years, p. 173-182. *In* B.J. Rothschild (ed.) Toward a theory on biological-physical interactions on the world ocean. Kluwer Academic Publications.

Leong, R.J.H. and C.P. O'Connell. 1969. A laboratory study of particulate and filter feeding of the northern anchovy (*Engraulis mordax*). J. Fish. Res. Board Can. 26: 557-582.

MacCall, A.D. 1980. The consequences of cannibalism in the stock-recruitment relationship of planktivorous fishes such as *Engraulis*, p. 201-220. *In* G.D. Sharp (ed.) Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, Lima, Peru, April-May 1980. IOC Workshop Rep. 28. UNESCO, Paris. 323 p.

Mais, K.F. 1974. Pelagic fish surveys in the California current. Calif. Dep. Fish. Game, Fish. Bull. 162. 79 p.

Mathisen, O.A., R.E. Thorne, R.J. Trumble and M. Blackburn. 1978. Food consumption of pelagic fish in an upwelling area, p. 111-123. *In* R. Boje and M. Tomczak (eds.) Upwelling ecosystems. Springer-Verlag, Berlin.

Mayr, E. 1982. The growth of biological thought. Harvard University Press, Cambridge, Massachusetts.

McFarland, W.N. and S.A. Moss. 1967. Internal behavior in fish schools. Science 156: 260-262.

Mendelssohn, R. and J. Mendo. 1987. Exploratory analysis of anchoveta recruitment off Peru and related environmental series, p. 294-306. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Resources Management (ICLARM), Manila, Philippines.

Miller, T.J., L.B. Crowder, J.A. Rice and E.A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Can. J. Fish. Aquat. Sci. 45: 1657-1670.

Muck, P. and G. Sánchez. 1987. The importance of mackerel and horse mackerel predation for the Peruvian anchoveta stock (a population and feeding model), p. 276-293. *In* D. Pauly, and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Murphy, G.I. 1973. Clupeoid fishes under exploitation with special reference to the Peruvian anchovy. Tech. Rep. No. 30, University of Hawaii, Hawaii Institute of Marine Biology. 73 p.

Palomares, M.L., P. Muck, J. Mendo, E. Chumán de Flores, O. Gómez and D. Pauly. 1987. Growth of the Peruvian anchoveta (*Engraulis ringens*), 1953 to 1982, p. 46-74. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D. 1981. The relationship between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. Meeresforsch. 28(4): 251-282.

Pauly, D. and I. Tsukayama, Editors. 1987. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Parker, R.R. 1981. Size-selective predation among juvenile salmonid fishes in a British Columbia inlet. J. Fish. Res. Board Can. 28: 1503-1510.

Pitcher, T.J. 1986. Functions of shoaling behavior in teleosts, p. 294-337. *In* T.J. Pitcher (ed.) The Behavior of Teleost Fishes. John Hopkins University Press, Baltimore.

Pulliam, H.R. and T. Caraco. 1984. Living in groups: Is there an optimal group size? p. 122-142. *In* J.R. Krebs and N.B. Davies (eds.) Behavioral ecology. Second edition. Blackwell, Oxford.

Sibly, R.M. 1983. Optimal group size is unstable. Anim. Behav. 31: 947-948.

Smith, P.E. 1970. The horizontal dimensions and abundance of fish schools in the upper mixed layer as measured by sonar, p. 563-591. *In* G.B. Farquhar (ed.) Proceedings of the International Symposium on Biological Sound Scattering in the Ocean. Maury Cent. Ocean Sci., Dep. Navy, Washington, DC.

Smith, P.E. 1981. Fisheries on coastal pelagic schooling fish, p. 1-32. *In* R. Lasker (ed.) Marine fish larvae. Washington Sea Grant Program, University of Washington Press, Seattle.

Steele, J.H. 1974. The structure of marine ecosystems. Harvard University Press, Cambridge.

Ware, D.M. 1980. Bioenergetics of stock and recruitment. Can. J. Fish. Aquat. Sci. 37: 1012-1024.

8902

Memorias del Simposio Internacional de los Recursos Vivos
y las Pesquerías en el Pacífico Sudeste
Viña del Mar, 9-13 mayo, 1988

Comisión Permanente del Pacífico Sur (CPPS).
Rev. Pacífico Sur (Número Especial), 1989

RECRUITMENT IN FISHERY RESOURCES AND ITS RELATIONSHIP TO ENVIRONMENT: ACCESSIBLE PATHWAYS TO GREATER INSIGHT

ANDREW BAKUN
Pacific Fisheries Environmental Group, Southwest Fisheries Center
National Marine Fisheries Service, NOAA
P.O. Box 831, Monterey, California 93940, U.S.A.

Abstract

Scientific progress in the resistant problem area of recruitment variability in exploited fish populations may depend on the ability to move beyond the restrictive paradigm that has provided the framework for many previous advances in fisheries science Rather than aggregating information temporally and spatially into composite annual data points, it appears necessary to specifically address the richly detailed temporal and spatial patterns which exist within seasonal periods and within the same, and among different, regional habitats

Coherent conceptual frameworks, within which generic questions can be posed, are needed. Well-posed high resolution studies, such as the SARP "within-year" exercises along with complementary high spatial resolution observational exercises, offer rational approaches to addressing certain key questions. Broad application of the comparative method of science is advocated. Interpretation of behavioral adaptations to environmental circumstances potentially constitutes a powerful inferential tool. It is suggested that particulary amenable fish population and habitat settings be utilized in addressing key generic questions in order to support broadly-based multilateral scientific progress

INTRODUCTION

Lack of scientific understanding of the mechanisms controlling recruitment variability constitutes the key problem area in fishery science at the present time (the term "recruitment" referring to the quantity of younger fish surviving the various egg, larval, and juvenile stages to begin to be captured in a fishery). Recruitment in most fish populations is found to vary erratically from year to year in ways that presently cannot be explained or predicted. The problem remains largely unsolved after many decades of dedicated scientific effort by highly capable scientists in a number of nations around the world.

The result is a situation in which those involved in fishing and associated industries must deal with chronic uncertainties as to the year-to-year fluctuations in the abundance of the fish populations on which they depend. However, even more importantly, the unexplained large-amplitude interyear variability obscures the essential underlying signals needed to foresee and manage the effects of fishery exploitation over longer time scales. These signals include the functional form of the relationship of expected recruitment to stock size, trends in stock productivity, interspecies interactions, effects of climatic change or habitat alterations, etc. Lacking the ability to resolve these signals, the methodologies of fishery science must rely on arbitrary assumptions and extreme simplifications concerning the very factors which control the important long term outcomes (such as the possibility of eventual displacement of a fished species from a position in the biological community wherein it constitutes an economically viable resource). The smooth functional curves drawn through erratic scatters of data points, which are often the products of these conventional methodologies, tend to be neither intellectually convincing nor operationally reliable. Collapses of important fishery stocks around the world continue to occur, with attendant socioeconomic consequences. Real improvement in the situation does not appear likely until significant advances in scientific understanding of the mechanisms controlling recruitment variability can be realized.

Since "recruitment" is the net result of a chain of life cycle events extending from the formation of reproductive product within the adult fishes, through the various egg, larval, and juvenile stages, it typically reflects not a single process but a large number of interacting processes by which huge numbers of tiny eggs undergo drastic reduction to very much smaller numbers of surviving recruits. In passing through these stages, an individual grows through a great range in size, and so an identical process may affect its survival in different ways at different stages in its development. During this period, the organisms are essentially invisible to humans because they are not taken by any fishery. Thus it is undeniably expedient, in an operational sense, to treat this entire period in terms of the single aggregate quantity, "recruitment". However it is not surprising that this approach has not generally yielded simple, constant relationships either to parental stock size or to environmental conditions.

Straightforward step-by-step application of the experimental method, in the classical scientific tradition, has not yielded major penetration of the problem. Valid experiments on the processes regulating survival of larval or juvenile fishes tend to be very difficult to accomplish. This is because conditions in the ambient ocean environment are not amenable to experimental controls and also because the mixture of scales of motion in the ocean makes it impossible to maintain the integrity of the volume of water in which an experiment is taking place unless it is contained in some way. However, any sort of artificial containment restricts the scales of the processes, and also imposes unrealistic interfaces and substrates, such that essential mechanisms tend to be altered. But of all the experimental difficulties, probably the most serious is the fact that, because of the enormous reduction in numbers that occurs, survival of any individual to the stage at which recruitment takes place is a very rare event with respect to the fate of the overwhelming majority of hatchlings. Thus, the circumstances affecting a given sample of quite typical larvae may be quite irrelevant to eventual recruitment to the population; that is, it may well be that only very small subgroups of quite non-typical larvae that find themselves in very special circumstances are the only ones with any prospect at all of survival. Thus even if valid result could be obtained for an experimental sample, these are likely to bear no relationship at all to the net recruitment observed at the population level. Thus, in order to achieve unequivocal results, experiments need to be performed at the population level; and if experiments on sample segments of a population are difficult, the problems involved in addressing a population as a whole tend to be overwhelming. For these reasons, most recruitment research in the past has followed the empirical approach, whereby statistical relationships are sought between the total integrated result, i.e. "recruitment", and various indices of aggregate environmental circumstances or population size.

A major problem with the empirical approach is the fact that the lack of understanding of the causal mechanisms presents far too many choices of variables and formulations to be effectively sorted out with the relatively short lengths of available data series. There are always a multiplicity of potential linkages of environmental processes and conditions to survival of young fish available for consideration. A variety of oceanographic, meteorological, or proxy time series can be constructed and associated with one or more of these linkages. Various uncertainties as to appropriate time scale, temporal lag between cause and effect, etc., multiply the possibilities for constructing explanatory data series. By searching through the range or possibilities, some degree of correlation with short (usually autocorrelated) time series of annual data points can often be found and then readily justified according to one or another ecological mechanism. When such a correlation happens to be high enough to meet standard significance criteria, it becomes "publishable" as an advance in scientific understanding, whereas slightly weaker correlations do not. This happens even though given the multitude of possible interactions with growth, predation, transport, physiological stress, etc., occurring at various life cycle stages, it may seem nearly inconceivable that any one mechanism could so dominate survival as to yield a strong univariate correlation that was not at least to some degree spurious. Even if the search through the possibilities of explanatory variable formulations proceeds over a period of time via independent efforts of a number of different researchers, each with a separate *a priori* hypothesis, and each scrupulously limiting himself to a single *a priori* choice of explanatory variables, the problem is not alleviated. Only successes are generally published, and so the ratio of successes to non-successes is unknown. Therefore, a statistical basis for judging the likelihood that a particular reported "relationship" may be spurious, is lacking. Thus, we have the situation that most of the empirical environment/recruitment relationships published in the scientific literature are probably at least to some degree spurious, with others that may have represented realistic degrees of actual linkage having been discarded as not meeting significance criteria (Bakun, 1985).

As a result of the respective difficulties involved in the experimental and empirical approaches, fishery-environmental science is not well-developed at the present time. Perceiving this less than satisfactory situation, fish population dynamicists have tended either to ignore environmental variation altogether or to treat it in unrealistic ways (e.g.,as merely random variability about some steady base level, etc.). Indeed, some (e.g., Walters, 1984; Butterworth et al.[1]) have become sufficiently discouraged to suggest that studying the causes of recruitment variation may ultimately turn out to be futile and that research funds might be better spent on other problem areas.

Such a lack of optimism is disconcerting in its apparent implication that what we call "fishery science" is somehow fundamentally different from other sciences wherein the existence of generalizable laws and principles, capable of being identified through application of the scientific method, is taken for granted. And it would seem to relegate fishery science to a somewhat permanent status of being more in the nature of an operational "craft" than of a true prognostic science. Nevertheless, it is a fair question and these authors can in no way be faulted for posing it. And, it should be acknowledged that by "futile" they undoubtedly mean to imply "futile at any justifiable level of research funding".

In fact, the analyses of Walters and of Butterworth et al. present compelling arguments under the conventional paradigm within which they are posed. An axiom of that paradigm is the idea that each "unit stock" exists in such a unique biological and environmental setting that the only information useful for analysis and prediction is that derived directly and exclusively from the particular stock in question. In addition, fish are mobile and live in a moving fluid environment, thereby blurring spatial distinctions within the stock habitat. Also the seasonal variation is of such dominance in most biological processes that interference of seasonal effects tends to distort subannual time series. As a result the conventional practice has been to aggregate all the data of a given type that may be available within a particular year into a single annual data point. This paradigmatic view has served as the primary conceptual framework for fishery science for a number of decades, providing the basis for its major operational accomplishments (e.g., yield-per-recruit estimation, surplus-productions models, stock-recruitment relationships, etc.). So it is not surprising that there is a strong inclination among fishery scientists to couch the recruitment variability issue within the same frame of reference.

The arguments of Walters (1984) and Butterworth et al.[1] provide the valuable service of clearly pointing out that in order to develop crucially-needed improved insight into the recruitment question it may be inescapable that this restrictive paradigm must be relinquished and legitimate ways to move beyond it found. Actually, this broadening of viewpoint is already well underway. There have been recent indications of the utility of the comparative method of science, as applied to appropriate groupings of different stocks and environmental setting (e.g., Bakun, 1985). And recent technological developments have led to the development of high-resolution (both temporal and spatial) approaches to the problem (e.g., Lasker, 1988;) Buckley and Lough, 1987) thereby resolving the "single aggregate data point per year" dilemma. We have a new global scientific program, the International Recruitment Program (IREP), established within the Program of Ocean Science in Relation to Living Resources (OSLR) which is co-sponsored by the Intergovernmental Oceanographic Commission (IOC) and the Food and Agriculture Organization of the United Nations (FAO). IREP is being specifically designed to facilitate multinational collaboration in, and to thereby maximize effectiveness of, both the comparative and the high temporal/spatial resolution approaches. One of the focal projects within IREP, the Sardine-Anchovy Recruitment Project (SARP), has been established to focus particular attention on the high-resolution aspect, although the interregional comparative approach is also incorporated as an important element of the SARP project design.

POSING GENERIC QUESTIONS

It appears that the route to progress may lie, rather than in attempting to solve the recruitment question completely and independently in any one regional system, in being able to find ways to break the problem down to certain key generic questions, as well-posed and amenable to multilateral scientific effort as possible, that will facilitate a broadly based step-by-step accumulation of insight. As such increases in insight might accrue, they would not only be available for direct application to management concerns but could provide guidance as to proper design and allocations of subsequent research effort.

I would here like to cite two recent studies. The first is the recent paper by Peterman and Bradford (1987) which suggests that early stage survival of anchovy larvae off California is related to the frequency of periods of calm winds during the spawning season (Fig. 1). The conclusion one would draw is that reproductive success may be related to rather short-term, somewhat random events in the manner or the hypotheses developed by Reuben Lasker and his co-workers at La Jolla (e.g., Lasker, 1978,1981a,1981b,1988). In such a case, a

---

Butterworth D.S., Bergh M O . Sparks R Prospects for incorporating enviromental and species interaction effects in Benguela pelagic resource projections -presented at the Symposium on Population and Community Ecology in the Benguela Upwelling Region and Comparable Frontal Systems. Cape Town. South Africa. 8-12 September. 1986

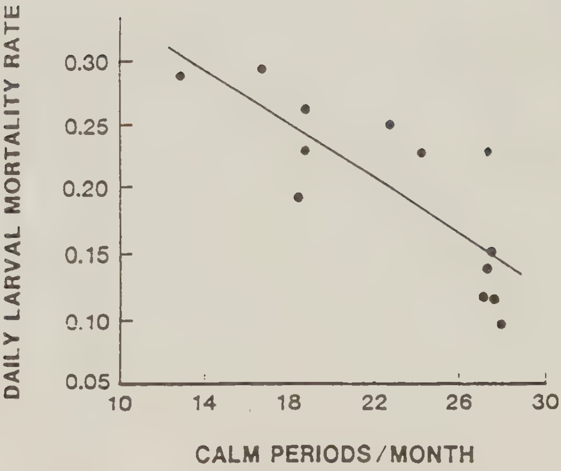


Fig.–1 Correlation between frequency of calm periods and mortality rate of recetly hatched northern anchovy larvae (*Engraulis mordax*) off California (after Peterman and Bradford, 1987, reprinted with permission of *Science*, Copyright 1987 by AAAS)

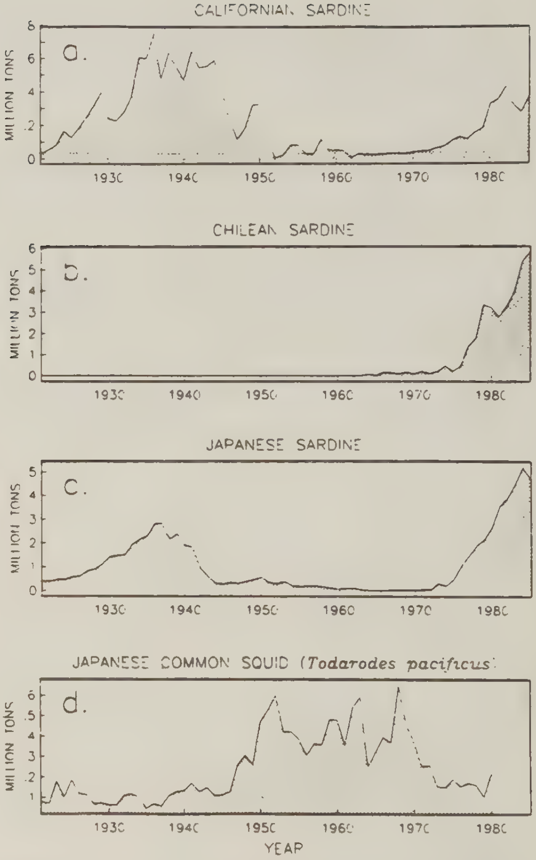


Fig.–2 Time series of sardine catches in the (a) northeastern Pacific, (b) southeastern Pacific, and (c) northwestern Pacific Ocean and of catches of (d) *Todarodes pacificus* (winter spawning population) in Japanese waters. (Note that the scales for panels 'a', and 'd' are expanded relative to those of panels 'b' and 'c' by factors of about ten. Also note that in the earlier peak shown in panel 'a', catches were largely from the northern subpopulation inhabiliting the region off the western U.S.A., while the recent catches are largely from a subpopulation existing within the Gulf of California and include catches of other pelagic species. Panels 'a','b' and 'c' are adapted from Kawasaki, 1983, with the addaption of more recent data kindly provided by Dr. Kawasaki. Panal 'd' is adapted from Hatanaka et al., 1984.)

single annual composite environmental descriptor would obviously be inadequate to demonstrate the linkage; moreover, where more than one type of short term effect might be acting at different times within a season, aggregating the information in annual composites would tend to hopelessly confound the analysis.

Next I would like to cite Kawasaki's (1983) paper which called attention to the fact that sardine populations off California, off Chile, and off Japan seem to have grown and collapsed in synchrony (Fig. 2a,b,c). Kawasaki suggested subtle, very long-term, oceanwide environmental changes which must somehow affect these very widely separated populations similarly. In this case, the suggested oceanwide environmental changes must have been quite subtle, since no clear evidence of directly corresponding fluctuations has (to the knowledge of this author) yet been reported in the available marine climatic data. Therefore, one would think that they would have to be too subtle to control such explosive population expansions and collapses by direct effects on the sardines themselves. And so one would tend to think of complex reorganizations of the biological community structure in the ocean perhaps in response to chronic, long-term, low-level environmental changes.

At the present time one really cannot say which is generally more important in controlling fish population dynamics: short term, rather stochastic evironmental events directly affecting reproductive success, or longer-term chronic effects, perhaps acting by way of changes in the composite marine biological community structure. The question is certainly a salient one, from both the research and management points of view. If the environmental controls are direct, it might be reasonable to attempt to manage a stock somewhat in isolation, directing effort toward insuring maintenance of sufficientspawning population to take advantage of rather randomly occurring opportunities for excellent reproductive success. However, where the controls may act through biological community interactions, it might be well to direct some serious study to the possibility of beneficial intervention by purposefully impacting selected components of the interlinked biological system. For example, R.K. O'Dor, of the cephalopod International Advisory Council (CIAC), has pointed out that the explosive rebirth of the Japanese sardine stock directly coincided with the collapse, under heavy fishery pressure, of the very large stock of oceanic squid, *Todarodes pacificus*, in the region (Fig. 2d). Such squids are undoubtedly voracious and efficient predators on small pelagic fishes, growing to full size and completing their entire life cycle within one year (Hatanaka et al., 1985).

The SARP Concept

The SARP temporal-resolution "within-year" exercise (often referred to simply as the "SARP Experiment"), developed under the leadership of Reuben Lasker and his colleagues at Southwest Fisheries Center, has been identified (e.g.,Anon.,1983,1984, 1987) as the most promising experimental approach presently available for addressing the mechanisms and impact of short term temporal variability in larval survival *at the population level.* As mentioned earlier, other types of potential experiments suffer from the fact that because of the enormous reduction in numbers of individuals during the early life stage, recruitment may depend on small subsets of very non-typical larvae; the fate of typical larvae may be quite irrelevant. The key attribute of the SARP concept is its reliance upon capturing survivors, i.e., members of the successful subset, at a later life cycle stage and then reconstructing its exact birth date, and also indications of its growth history, from daily marks carried in the bony structures (Pannela, 1971; Methot, 1983; Campana and Neilson, 1985). These would then be compared to short term variability in environmental processes and conditions, utilizing such techniques as histological measures of starvation (Theilacker, 1986) and immunoassays of predator stomach contents (Theilacker et al.,1986) as diagnostic tools, to reveal the causal mechanisms.

Thus,the exercise constitutes a "natural experiment", wherein advantage is taken of naturally-occurring environmental variation rather than relying on controlled manipulation of conditions. Implicit in the procedure is a loss of spatial resolution, because the animals are mobile during the period between birth and capture; this may not a crucial drawback because the most energetic sources of short term variability (atmospheric storms, etc.) affecting the upper ocean environment tend to be of rather large spatial scale.

In order to produce a valid "survival index" from larval birthdate frequencies it is necessary to adjust for short term variability in larval production, which may occur on rather finely detailed spatial scales; thus a full SARP "within-year" exercise requires detailed monitoring of larval production over the entire reproductive habitat at short (one-to two-week) intervals over the major portion of an extended spawning season. The full exercise therefore implies a sizable commitment of resources for at-sea operations that has been difficult to achieve under the funding constraints of recent years.

This has led to suggestions (by J. Alheit and others) that the SARP context be broadened to include other types of high-resolution (both temporal and spatial) studies. Besides yielding important new insight on their own, such studies would also serve to maximize the scientific value of the relatively few full SARP "within-year" exercises that can be expected to be accomplished, around the world, within the next few years.

Technologies for indicating short term larval growth rates, both biochemically (Buckley, 1984) and by measurement of daily otolith increment width (e.g., Gutiérrez and Morales-Ninn,1986), appear to be applicable in the SARP context. While not yielding "survival" directly, growth rate probably regulates survival to a large degree. The major sources of larval mortality appear to be starvation and predation (Hunter,1981). Starvation and growth rate are obviously related. Vulnerability to predation appears to be highly size-dependent (ibid.) and so predation mortality can also be considered to be closely linked to growth rate.

If the growth rate history recorded in the daily otolith increments can be appropriately utilized, some of the attributes of the high temporal resolution SARP experiment may be realizable at a fraction of the at-sea survey cost of the full SARP "within-year" exercise. This is because such a growth record does not necessarily require the repeated detailed surveys of larval production that are required to convert birthdate frequencies to an index of survival. It may be possible to draw useful conclusions from as minimal a field effort as collecting several representative samples of late larvae or juveniles, reconstructing the sequence of characteristic growth rate variability (adequately replicated among acceptably independent samples), and simply comparing the sequence to such readily apparent large-scale events as storm occurrences.

An alternate technique for indicating relative differences in growth rate, i.e., which utilizes RNA - DNA ratios (Buckley, 1984), does not yield a temporal record from any sample. It reflects only very recent growth, on the several-day time scale. However, the necessary close linkage in time also implies a corresponding close linkage in space; and so spatial resolution, lost in the full SARP "within-year" exercise, is recovered. Important habitat structure exists on relatively small scales in both the vertical and horizontal dimensions. Appropriate sampling of larvae with respect to such structure, and determining abundance and nutritional state as reflected in recent growth rate, could yield rich material for drawing mechanistic inferences. Additional diagnostic tools such as the histological and immunoassay techniques mentioned above could also be employed. Satellite imagery would be an aid in defining horizontal structure at the sea surface. This could be related to vertical structure in ocean properties and flow by means of physical oceanographic theory (and by use of sonic of *in situ* profiling techniques, etc., where available, during the sampling operation).

Such high spatial resolution studies are another example of a "natural experiment" which utilizes natural variation, in this case in the spatial dimension, as a substitute for controlled experimental manipulation. Spatial studies of this type could yield valid conclusions concerning mechanisms regulating larval survival without the requirement for repeated detailed characterization of an entire reproductive habitat which is such a demanding feature of the full SARP "within-year" experiment. They could also serve to "fill in" our understanding of spatial aspects needed to derive the maximum insight from those temporal SARP studies (wherein spatial resolution is lost) that can be implemented.

THE COMPARATIVE METHOD

"Natural experiments" such as discussed above, which take advantage of natural variability to produce distinct realizations of the processes being investigated, actually constitute applications of the comparative method of science. Mayr (1982) identifies the experimental method and the comparative method as "the two great methods of science" and in fact bases the distinction between them on whether or not there is controlled manipulation of the experimental conditions. He cites the revolutionary advances in evolutionary biology, based nearly entirely on the comparative method, as an example of its power. Since the ocean environment is basically uncontrollable, and certainly so on scales affecting important fishery species at the population level, it would seem to make sense to look to the comparative method as one clearly operable route toward scientific progress on the recruitment question.

Bakun (1985) presented a rationale for addressing the recruitment issue by means of interregional comparative studies of two particular types: (1) comparisons of environmental characteristics of reproductive habitats of stocks of the same or similar species in order to infer the dominant common factors affecting reproductive success, and (2) comparisons of empirical model formulations as a means to enhance confidence in statiscally-weak relationships and to detect spurious ones.

Parrish et al. (1983) provide an example of the first type of approach; in examining the seasonal and geographical characteristics of the four major subtropical eastern boundary current regions of the world's oceans, they found a general pattern of avoidance of intense wind-induced turbulent mixing and of strong offshore-directed surface Ekman transport in the spawning habits of anchovies and sardines. Temperature at which spawning takes place showed a much less coherent pattern, suggesting that selection of spawning habitat on the basis of a particular optimum temperature is less important than minimizing turbulent mixing (dissipation of food particle concentrations) or offshore transport (loss of larvae from the coastal habitat).

Cury and Roy (in press) provide a most illuminating example of the power of the second type of approach. They investigate the empirical response of interyear variation in recruitment success of pelagic fishes to interyear variation in alongshore wind intensity in several different regional settings (Perú, California, Morocco, Senegal, and Ivory Coast) and find a characteristic "dome" shape in the response, such that very low wind speeds (too little upwelling) and high wind speeds (too much offshore Ekman transport and turbulent mixing) are unfavorable, with optimal survival tending to occur at intermediate wind speed values (peaking at a root-mean-square value of about 5-6 m/sec). In the case of the Ivory Coast, where the upwelling is not substantially wind-induced on the local scale and therefore not linked to local offshore Ekman transport, Cury and Roy found recruitment success to increase monotonically with upwelling intensity.

Certainly, additional types of comparative approaches are available. The crucial ingredient is an appropriate conceptual framework within which the data can be arrayed in ways that reveal informative patterns (i.e., so as to constitute reasonable "natural experiments"). Cushing's (1975) "match-mismatch" hypothesis has been useful in this regard. Lasker's (1981b) "stable ocean" hypothesis has provided conceptual underpinning to many of the examples cited in this paper, as has the "offshore transport" hypothesis of Parrish et al. (1981).Sinclair's (1988) "member/vagrant" hypothesis presents a rich set of ideas concerning population pattern, size, and temporal variability.

Bakun (in press) advanced a particular hypothetical view of trophic interaction in the ocean, wherein large-amplitude interyear variability in reproductive success, largely due to "weak links" in the life cycle, constitutes an integral component of the time-space pattern a fish population presents in order to maintain its "living space" within the trophic pyramid. Such a "high-risk" strategy, which might result in frequent reproductive failure when conditions are not highly favorable (i.e., indice large-amplitude interyear variability), may allow a species to establish itself as a dominant component of an ecosystem under particulary favorable circumstances and then persist in its dominance over longer time scales through the action of several density-dependent mechanisms that may favor it over less abundant, suppressed species.

The point to be made is that such hypothetical statements and conceptual views, while they are undeniably speculative and necessarily oversimplified, offer guides for structuring available information in narrowed, more focussed contexts so that a comparative study can to a lesser degree constitute an exercise in circular reasoning (i.e., avoiding falsification by continually adjusting the premise to accommodate conflicting data) and to a greater degree represent a well-posed "natural experiment". Because of the predilections of fishery scientists to view each regional situation as unique, examples of such focused comparative analysis are rare in this field. It seems likely that substantial insights could accrue from simply assembling the various fragments of data and experience that are already available, arraying these according to specific conceptual frameworks, and looking for informative patterns of consistency and disparity.

We have an impressive recent example of cooperative assembly and integrative analysis of various types of data series in the IMARPE/GTZ/ICLARM Anchoveta Ecosystem Study (Pauly and Tsukayama, 1987). It seems that this study can serve as a model for similar efforts in other areas around the world. If so, one effect would be to encourage and facilitate broad application of the comparative method. By offering its experience and results for incorporation in a wider comparative context each such effort could thereby realize enhanced scientific utility in terms of its own local fishery concerns, while in turn expanding the available suite of potential comparative analogues and thereby contributing to the general scientific benefit all of the associated regional efforts.

LOOK AT THE ORGANISMS AND WATCH WHAT THEY DO

Active movement within the liquid ocean environment exacts a significant caloric cost; moreover this cost is relatively higher for smaller organisms because of size-dependent hydrodynamic factors. A fish population occupying a dominant position within its particular trophic level would tend to be one that could excel at dealing energetically with the spatial and temporal pattern presented by its food sources, while presenting a pattern to its predators that imposes a sufficient energetic cost to defeat growth of intolerable levels of predation pressure (Bakun, in press). Certainly, since vulnerability to predation may decrease with increasing size (Hunter, 1981), a great premium must be placed on conserving energy so that as much as possible can be used in maximizing growth rate, particularly in the case of early stages. Likewise, it will be important for mature adults to conserve energy for maximizing production of gonadal material.

Since survival and reproductive success are the factors which drive natural selection, it is logical that any observed adaptations which involve substantial energy expenditures must be strongly linked to mechanisms exerting major control on these factors. Thus, one can argue that consistent behavior patterns involving directed active movement by the organism must in no way be mere capricious quirks, but are reflective of adaptive responses to processes or conditions which regulate recruitment (i.e. net reproductive success and survival to adulthood of the progeny, at the population level). Thus it is reasonable to look to such behavior patterns as clear indicators of the identity of the predominant processes controlling recruitment variability.

For example, Parrish et al. (1981) noted that coastal pelagic fishes of the California Current, which feed as adults in the upwelling region off northern California and in the richly productive regions even further to the north, migrate long distances to the Southern California Bight to spawn. By contrasting the conditions in the reproductive habitat and in the distant feeding grounds, and by utilizing certain other evidence, they arrived at the conclusion that avoidance of offshore transport and associated loss of larvae from the coastal habitat was a major factor controlling reproductive success (i.e., important enough to be worth the long migration). This finding has provided an independent rational basis for some successful empirical tests of recruitment success against indices of offshore transport in the larval habitat; these tests are cited by Shepard et al. (1984) as one of the few indications to date of positive progress in linking variations in fish stocks to environmental effects.

On a much smaller spatial scale, the high spatial resolution studies discussed earlier in relation to the SARP project could involve a similiar inferential rationale in cases where active swimming may be deemed to account for spatial patterning in the concentration of larvae. However, because of the limited swimming ability of early life stages, their ability to exert control on their location by directed swimming behavior in the horizontal plane, except on the very smallest scales, tends to be slight. Thus, the horizontal distribution of larvae may be largely reflective of random, somewhat accidental displacements, rather than of adaptive behavioral responses. Therefore the horizontal larval distribution in itself may offer limited unequivocal information as to mechanisms regulating survival on the population level. This is the reason that a high spatial resolution study may need other criteria in addition to the distribution of larval abundance, such as afforded by the various techniques to indicate recent growth and nutritional state cited earlier, to yield informative inferences from horizontal pattern in environmental and biological processes.

However, if the focus is shifted to address pattern in the vertical dimension, the situation is quite different. Even small, feebly swimming organisms can exert substantial control on their vertical position in the water column. Thus directed behavioral adaptations can significantly counter fortuitous displacements in the vertical, with the result that vertical pattern in larval distribution may represent a quite clear signal that is relatively free of unrelated random noise that could obscure evidence of adaptive conformity to environmental mechanisms. Most flow processes affecting larval transport in the ocean are characterized by significant vertical shears. The hydrodynamical mechanisms involved are fairly well understood by physycal oceanographers. Bakun (1986) surveys these mechanisms and provides references for more detailed treatment; also see additional discussion by Bakun (in press). These hydrodynamic mechanisms afford a ready conceptual framework for analyzing the function of vertical migratory behavior, concentrations in vertical strata, etc., by larvae. And to reiterate, evident adaptive conformity to one of these mechanisms may be taken as indication that the particular mechanism is important to reproductive success and therefore a factor in recruitment variability.

In the past, sampling of fish larvae has been often directed primarily toward estimating gross abundance or toward general delineation of spawing grounds, and so vertical structure in the distribution of larvae has commonly been viewed merely as irrelevant detail and an unwanted source of sampling error. As a result, a standard practice in fisheries work has been to integrate this structure by use of vertical or oblique net tows. For this reason, there is presently relatively little information available on vertical pattern in larval distributions, even for well studied fish stocks. However, the necessary sampling gear and techniques are available, as are new sonic techniques for describing vertical profiles of current velocity. And there is growing recognition that fish larvae commonly manage to undergo drift trajectories that are distinctly different from those which inert drifting particles must follow (Bakun, 1986; Sinclair, 1988). The conclusion is that vertical migratory behavior, interacting with vertical structure in the flow field, often constitutes a key ingredient in life cycle closure and, to the extent that this closure is dependent on a varying flow field, in recruitment variability. Thus, mere assembly of a set of observations of vertical distribution of larvae, covering a range of conditions which might affect flow characteristics, might provide a basis for an inferential process leading to important insights into factors controlling both interyear and spatial scale of recruitment (Bakun, 1986).

In summary, the adaptive responses which we observe in the behaviors and life cycle activies of marine organisms may be viewed as the integrated result of a great number of "trial and error experiments" performed by their populations. As such, they may represent rather clear signals of the primary mechanisms affecting reproductive success which are relatively uncontaminated by short term, large amplitude, quasi-random "noise"imposed by environmental fluctuations or by associated transients in the biological community structure. Thus, by looking at what the organisms habitually do under various circumstances, assuming we have an adequate conceptual framework for appropriately sorting out the circumstances, it may be possible to infer much about the nature and causes of population variability that might be very difficult to develop using more direct emperical or experimental approaches.

Multilateral collaborative effort

As indicated above, the salient question is not whether the recruitment problem is intrinsically solvable (i.e., with unlimited research resources), but rather how to achieve badly needed progress under the stringent funding constraints generated by current economic circumstances. It has been argued above that there are certain reasonable directions for productive research that might be followed at reasonable cost; these can generally be expected to be most illuminating when pursued multilaterally in a number of systems of differing degrees of similarity. Key process-oriented at-sea exercices, such as the SARP "within-year experiment" are relatively expensive; obviously these cannot be duplicated in every major ecosystem of the word ocean.

We have recently applied the same methods previously used in our comparative study of eastern ocean boundary systems presented at the FAO Costa Rica Workshop (Parrish et al., 1983), to the western boundary areas of the South Atlantic[2, 3]. One finding of interest is that the sardinella of southeastern Brazil seems to be employing an identical strategy in its seasonal and locational adaptations, to solve a very similar set of environmental problems, to that of the sardine which spawns in the Southern California Bight. This is in spite of the very different environmental contexts represented by tropical versus temperate water temperatures and by the very different western boundary current versus eastern boundary current dynamical situations, and in spite of the separate genera (*Sardinella* versus *Sardinop*) involved. In our previous paper we found strong analogies between the reproductive strategies of the Southern California stock, and other eastern boundary current stocks which chose spawning habitats whithin coastal bights downstream of upwelling centers. Thus the Brazillian population would also appear to be quite analogous, with respect to environmental--reproductive linkages, to such other important sardine stocks as the spawning in the large coastal bight off northern Chile and southern Peru, and the Canary Current stocks spawning in coastal indentations near Casablanca, and near Sidi Ifni, Morocco.

The moderate size of the Brazillian population, and its relatively confined habitat located near ports and scientific institutions, may make it a particularly amenable setting for population-level recruitment experiments such as the "SARP Within-year" experiment. The recruitment question has certainly proven to be very resistant to scientific solution when addressed, inthe conventional manner, in the context of any single autonomous fish stock and habitat. The idea, that a few well-posed process-oriented experimental efforts mounted in paticularly amenable habitat settings could support and progressively advance a framework of comparative scientific insight, is undeniably atractive

There is a question of motivation and coordination and of such an altruistc multinational scientific attack on a common scientific problem area. The OSLR Programme being co-sponsored by IOC and FAO, and the International Recruitment Programme (IREP) established as its primary initial focus, have been mentioned earlier. Recently, the International Council for the Exploration of the Sea (ICES) has constituted an IREP Steering Group to promote collaborative action. France has established a National Recruitment Programme (PNDR). The U.S. National Marine Fisheries Service is in the process of re-orienting to an "ecosystem" research focus. A variety of other efforts by organizations such as SCOR, CPPS, Unesco, and various other international and national scientific agencies and institutions bear on the general problem area. The OSLR-IREP structure can potentially constitute a global collaborative framework of coordination of multilateral effort. Whether this can lead to tangible scientific progress may ultimately depend on the motivation of individual nations to commit resources to scientific project supportive of a broadly-based accumulation of generalized insight, rather than adhering to the conventional practice of viewing the problem exclusively within the restricted context of one's own particular regional marine ecosystem and fish stocks of local economic concern.

REFERENCES

ANONYMOUS. Workshop on the IREP Componet of the IOC Programme on Ocean Science in Relation to Living Resources (OSLR) -IOC Workshop Rep., 1983, vol. 33. Intergovernmental Oceanographic Commission, Unesco, Paris, 51 p.

ANONYMOUS. IOC-FAO Guiding Group of Experts on the Programme of Ocean Science in Relation to Living Resources, First Session -Reports of Meetings of Experts and Equivalent Bodies. N. SC -85/WS/18, 1984, Intergovernmmental Oceanographic Commission, Unesco, Paris, 34p

ANONYMOUS. IOC-FAO Guiding Group of Experts on the Programme of Ocean Science in Relation to Living Resources, Second Session-Reports of Meetings of Experts and Equivalent Bodies. N. SC- 87/ WS/ 41. 1987. Intergovernmental Oceanographic Comminssion, Unesco, Paris, 37p.

BAKUN A. Comparative studies and the recruitment problem: Searching for generalizations - CalCOFI Rep., 1985, vol. 26 p. 30-40

BAKUN A. Local retention of planktonic early life stages in tropical reef/bank demersal systems: the role of vertically-structured hydrodynamic processes - p. 15-32, in: D.Pauly and A. Yanez-Arancibia (eds.) IOC/FAO Workshop on Recruitment in

---

[2] Bakun A., Parrish R.H. Comparative studies of coastal pelagic fish reproductive habitats: the Brazilian sardine *(Sardinella aurita)* -MS

[3] Bakun A., Parrish R.H. Comparative studies of coastal pelagic fish reproductive habitats: the anchovy *(Engraulis anchoita)* of the south-western Atlantic -MS

Tropical Coastal Demersal Communities, IOC Workshop Report, 1986, vol. 40 (Supplement), Unesco, Paris, 323 p.

BAKUN A. L'ocean et al variabilite des populations marines -in: J.P. Troadec (ed.), L'Homme et les Ecosystems Halieutiques, Gauthier Villard, Paris (in press).

BUCKLEY L.J. RNA-DNA ratio an index of larval fish growth in the sea -Mar. Biol., 1984, vol. 80,p. 291-298.

BUCKLEY L.J., Lough R.G. Recent growth, biochemical composition, and prey field of larval haddock *(Melanogrammus aeglefinus)* and Atlantic cod *(Gadus morhua)* on Georges Bank -Can. J. Fish. Aquat. Sci., 1987, vol. 44, p. 291-298.

CAMPANA S.E., Neilson J.D. Microstructure of fish otoliths -Can. J. Fish. Aquat. Sci., 1985, vol. 42, p. 1014-1032.

CURY P., Roy C. Optimal environmental window and pelagic fish recruitment success in upwelling areas -Can. J. Fish. Aquat. Sci. (in press).

CUSHIING D.H. Marine Ecology and Fisheries -Cambridge Univ. Press, London, 1975, 271 p.

GUTIERREZ E., Morales-Nin, B. Times series of daily growth in *Dicentrarchus labrax* L. otoliths -J. Exp. Mar. Biol. Ecol., 1986, vol. 103, p. 163-179.

HANTANAKA H., Kawahara Y., Uozumi S.Y., Kasahari S. Comparision of life cycles of five ommastrephid Squids fished by Japan: *Todarodes pacificus, Illex Illecebrosus, Illex argentinus, Nototodarus sloani* sloani and noto todarus sloani gouldi NAFO Scientific Council Studues, 1985, vol. 9, p. 59-68.

HUNTER J.R. Feeding ecology and predation of marine fish larvae -p. 33-77, in: R. Lasker (ed.) Marine Fish Larvae: Morphology, Ecology and Relation to Fisheries, Univ. Washington Press, Seattle, 1981, 131p.

KAWASAKI T. Why do some pelagic fishes have wide fluctuations in their numbers? -biological basis of fluctuation form the viewpoint of evolutionary ecology -p. 1065-1080, in: G.D. Sharp and J. Csirke (eds.) Reports of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resource. FAO Fish. Rep., 1983, vol. 291, N. 1, 102p.

LASKER R. The relation between oceanographic conditions and larval anchovy food in the California Current: Identifications of the factors leading to recruitment failure -Rapp. P.-V. Reun. Cons. Int. Explor. Mer., 1978, vol. 173, p. 212-230.

LASKER R. Factors contributing to variable recruitment of the northern anchovy *(Engraulis mordax)* in the California Current: Contrasting years 1975 through 1978 -Rapp. P. -v. Reun. Cons. Int. Explor. Mer., 1981a, vol. 178, p. 375-388.

LASKER R. The role of a stable ocean in larval fish survival and Fish Larvae: Morphology, Ecology and Relation to Fisheries, Univ. Washington Press, Seattle, 1981b, 131p.

LASKER R. Studies on the northern anchovy; biology, recruitment, and fishery oceanography -p. 24-41, in: Studies on Fisheries Oceanography, Proceedings of the 25th Aniversary Symposuim "Fisheries and Fishery Oceanography in the Coming Century", Tokyo, November 10-13, 1986, Japanese Society of Fishery Oceanography, 1988, p. 24-42.

MAYR E. The Growth of Biological Thought -Harvard Univ. Press, Cambridge, Mass., 1982, 974p.

METHOT R.D.Tr. Seasonal variation in survival of larval northern anchovy *(Engraulis mordax)* estimated from the age distribution of juveniles -Fish. Bull. U.S., 1983, vol. 81, p. 741-750.

PANNELLA G. Fish otoliths: daily growth layers and perodical patterns -Science, 1971, vol. 173, p. 1124-1127.

PARRISH R.H., Bakun A., Husby D.M., Nelson C.S. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction -p. 731-778, in: G.D. Sharp and J. Csirke (eds.) Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, FAO Fish. Rep., 1983, vol. 291.1224 p.

PARRISH R.H., Nelson C.S., Bakun A. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr., 1981, vol. 1, N. 2, p. 175-203.

PAULY D., Tsukayama I. (eds.). The Peruvian Anchoveta and Its Upwelling Ecosystem: Three Decades of Change -ICLARM Studies and Reviews, vol. 15. Instituto del Mar del Peru (IMARPE), Callao, Peru: Deutsche Gesellschaft fur Techni - sche Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines, 1987, 351p.

PETERMAN R.M., Bradford M.J. Wind speed and mortality rate of a marine fish, the northern anchovy *(Engraulis mordax)* - -Science, 1987, vol. 235, p. 354-356.

SHEPARD J.G., Pope J.G., Cousens R.D. Variations in fish stocks and hypotheses concerning their links with climate -Rapp. P. -v. Reun. Cons. int. Explor. Mer, 1984, vol. 185, p. 255-267.

SINCLAIR M. Marine Populations -Univ. Washington Press, Seattle and London, 1987, 252p.

THEILACKER G.H. 1986. Starvation-induced mortality of young sea-caught jack mackerel, *Trachurus Symmetricus,* determined with histological and morphological methods -Fish. Bull. U.S., 1986, vol. 84, p. 1-17.

THEILACKER G.H., Kimball A.S., Trimmer J.S. Use of ELISPOT immunoassay to detect euphasiid predation on larval anchovy -Mar. Ecol. Prog. Ser., 1986, vol. 30, p. 127-131.

WALTERS C.J. Managing fisheries under biological uncertainty -p. 263-274, in: R.M. May (ed.) Exploitation of Marine Communities, Dahlem Konferenzen 1984, Springer-Verlag, Berlin, Heidelberg, New York, Tokyo, 1984, 366p.

8903

Alongshore Wind Stress, 1953-1984: Correction, Reconciliation and Update Through 1986

ANDREW BAKUN
ROY MENDELSSOHN
Pacific Fisheries Environmental Group
Southwest Fisheries Center
National Marine Fisheries Service, NOAA
P.O. Box 831, Monterey
California 93942, USA

BAKUN, A. and R. MENDELSSOHN. 1989. Alongshore wind stress, 1953-1984: correction, reconciliation and update through 1986, p. 77-81. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Abstract

Corrected values are presented for the monthly series of Peruvian alongshore stress presented in the previous volume of this series. The series is updated through 1986. The faulty "old" and corrected "new" series are compared and found to have very similar properties. It is concluded that studies based on the "old" series will not be significantly in error.

Resumen

Se presentan los valores corregidos del esfuerzo del viento a lo largo de la costa peruana, para las series mensuales dadas en el Volumen previo a este. La serie ha sido actualizada hasta 1986. Se compara la serie "antigua" defectuosa con la serie "nueva" corregida, encontrándose que ambas tienen propiedades muy similares. Se concluye que los estudios basados en la serie "antigua" no contienen error significativo.

Introduction

Bakun (1987) presented monthly indicator series for a number of environmental processes affecting the habitat off Peru. An error has been discovered in the computer program used to generate one of the reported series, that of the alongshore component of wind stress on the sea surface. Here we present corrected values for that particular series and also update the series through 1986 (Table 1).

Alongshore wind stress is one of the most important forcing functions for dynamic processes in the coastal environment. For periods of variation longer than a half-pendulum day (2.9 actual days at 10° latitude), the offshore transport which is directly driven by the wind (the offshore Ekman transport) is directly proportional to the equatorward alongshore wind stress, the constant of proportionality ($\sim 3.95 \times 10^4$ sec. for the latitude range of this particular series) being the reciprocal of the Coriolis parameter. To the extent that the flow divergence at the coast due to offshore surface transport is not balanced by convergence of alongshore flow, the water transported offshore is replaced by upwelling of deeper waters to the surface. Thus, variability in alongshore stress is reflected in variability in intensity of locally wind-driven coastal upwelling. Interyear variability in alongshore stress, often expressed either in terms of offshore Ekman transport or in terms of an "upwelling index", has been found to correlate with recruitment variability in a number of neritic fish populations (Bakun and Parrish 1980; Shepherd et al. 1984; Bakun 1985).

The computations and procedures employed in generating the updated corrected series (Table 1) are those outlined by Bakun (1987), except that the data for 1985-86 is from the COADS dataset rather than from the TDF-11 dataset.

Table 1. Alongshore component (positive equatorward) of wind stress on the sea surface. Units are dynes per square centimeter. Values in this table multiplied by the factor 3.95 yield offshore Ekman transport in cubic meter per second across each meter width.

Tabla 1. Componente a lo largo de la costa (positivo con dirección ecuatorial) del esfuerzo del viento sobre la superficie del mar. Las unidades se dan en dinas por centímetro cuadrado. Los valores de esta Tabla al multiplicarse por 3.95 dan como resultado el transporte Ekman en metro cúbico por segundo por cada metroo de línea costera.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	.33	.27	.37	.79	.70	.29	.63	.32	.42	.46	.55	.24
1954	.21	.37	.09	.41	.46	.40	.46	.73	.76	.21	.32	.19
1955	.32	.14	.50	.18	.54	.38	.41	.76	.57	.60	.54	.10
1956	.15	.23	.59	.70	71	.44	.59	.52	.57	.47	.40	.39
1957	.27	.43	.62	.71	.47	.66	.83	.51	.64	.49	.40	.51
1958	.36	.38	.40	.51	48	.41	.47	.67	.45	.42	.23	.34
1959	.30	.26	.34	.37	.26	.55	.33	.67	.45	.38	.27	.20
1960	.21	.24	.36	.42	46	.38	.51	.48	.45	.43	.29	.32
1961	.19	.22	.34	.41	.59	.41	.57	.42	.45	.58	.33	.27
1962	.38	.29	.41	.44	.43	.49	.52	.44	.53	.44	.45	.23
1963	.29	.34	.53	.40	.50	.28	.46	.40	.63	.62	.45	.32
1964	.43	.38	.44	.57	.52	.50	.53	.61	.64	.51	.31	.36
1965	.26	.35	.34	.46	.79	.50	.53	.70	.76	.55	45	.43
1966	.53	.53	.42	.61	.51	.53	.64	.65	.53	.48	.24	.22
1967	.34	.32	.25	.26	.33	.62	.48	.62	.62	.63	.39	.50
1968	.13	.35	.32	.30	.29	.55	.76	.63	.57	.53	.45	.50
1969	.26	.23	.39	.48	.39	.74	.49	.59	.52	.37	.26	.34
1970	.29	.11	.35	.50	.49	.45	.49	.45	.41	.47	.38	.26
1971	.16	.32	.29	.50	.35	.60	.39	.69	.53	.60	.38	.40
1972	.25	.27	.45	.47	.35	.58	1.00	.70	1.14	.44	.35	.65
1973	.52	.34	.60	.60	.57	.47	.58	.98	.85	.60	.49	.33
1974	.28	.35	.39	.57	60	.56	.61	.54	.65	.60	.59	.42
1975	.34	.31	.59	.51	.63	.53	.56	.77	.63	.46	.32	.31
1976	.19	.15	.42	.62	.61	.48	.50	.57	.70	.60	.54	.48
1977	.28	.46	.34	.49	.40	.56	.80	.69	.42	.41	.50	.46
1978	.33	.43	.54	.58	.50	.59	.53	.59	.63	.48	.45	.41
1979	.42	.45	.48	.59	.91	.76	.55	.70	.67	.56	.48	.43
1980	.39	.40	.42	.42	.73	.46	.81	.57	.63	.56	.42	.41
1981	.43	.25	.41	.46	.45	.71	.64	.52	.72	.37	.49	.34
1982	.32	.42	.52	.46	.57	.76	.76	.54	.80	.76	.84	.57
1983	.61	.55	.39	.63	65	.91	.70	.56	.62	.51	.33	.20
1984	.23	.56	.73	.27	.70	.79	.54	.78	.53	.51	.70	.47
1985	.27	.27	.16	.65	.48	.38	.50	.50	.65	.36	.52	.34
1986	.35	.23	.30	.41	.44	.56	.58	.68	.85	.75	.74	.44

Comparison and Reconciliation of the Two Series

Resolution of the alongshore component of the wind stress, τ_a, is according to

$$\tau_a = \alpha \tau_y - \beta \tau_x \quad \text{... 1)}$$

where τ_y and τ_x are the respective northward and eastward stress components; $\alpha = \cos\phi$ and $\beta = \sin\phi$, where ϕ is the angle, counterclockwise from true north, of the large-scale coastline trend. For the Peruvian coast a compass direction of 332° ($\phi = 28°$) is chosen as the characteristic large scale coastline trend (i.e., $\alpha = 0.8829$, $\beta = 0.4695$).

In producing the series reported by Bakun (1987), the value 0.8829, appropriate to α, was also erroneously assigned to β. Since the wind stress off Peru is generally from the southwest (Bakun and Parrish 1982), τ_x would generally have a negative value. Thus the magnitude of the monthly estimate of τ_a would tend to have been amplified by the error. The computation of the onshore component of the wind stress and of the "wind cubed" index (Bakun 1987) are unaffected by this error.

Thus the power spectra of the "old" series from Bakun (1987) generally has higher values than the "new" corrected series (Fig. 1a). However, note that the shape of the spectra are quite similar, with high peaks at the annual frequency and the familiar "red noise" spectral shape at the low frequency end. Note also that the coherence (Fig. 1b) between the series is very high, being nearly 1.0 over the spectral peaks and falling somewhat lower only in spectral "gaps" where very little of the variance of the series is found. Also there is essentially no phase difference between the two series over the entire spectral range (Fig. 1c). Fig. 1 shows that the two series should be nearly equivalent for most applications, except in terms of magnitude.

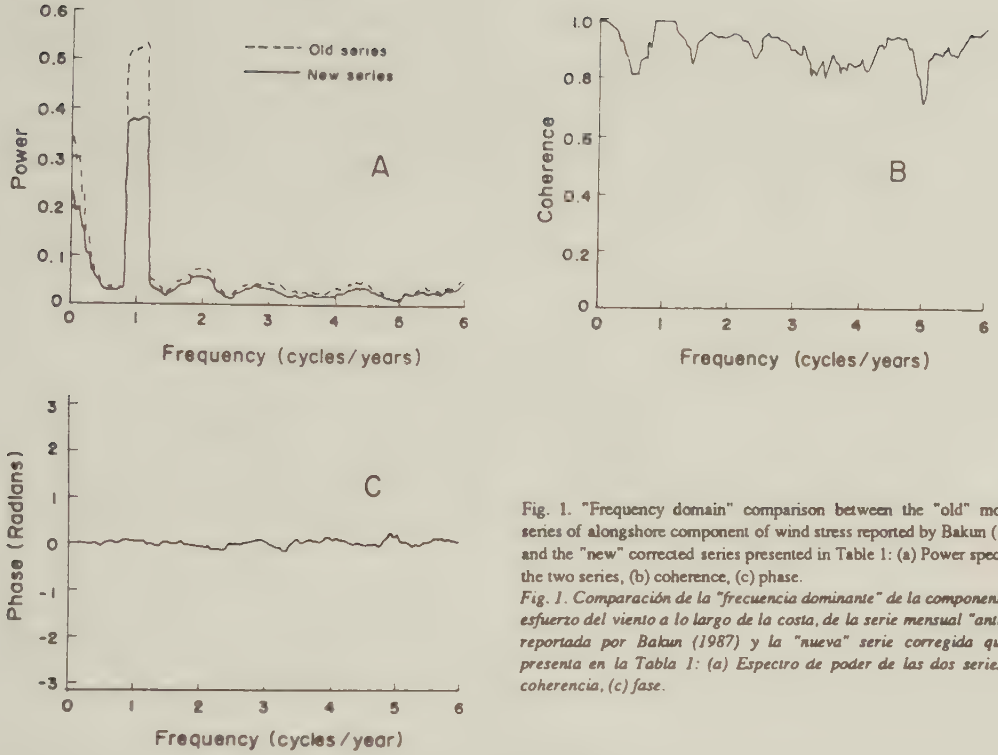


Fig. 1. "Frequency domain" comparison between the "old" monthly series of alongshore component of wind stress reported by Bakun (1987) and the "new" corrected series presented in Table 1: (a) Power spectra of the two series, (b) coherence, (c) phase.

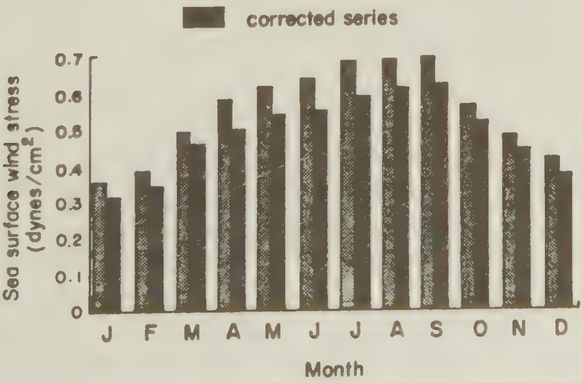
Fig. 1. Comparación de la "frecuencia dominante" de la componente del esfuerzo del viento a lo largo de la costa, de la serie mensual "antigua" reportada por Bakun (1987) y la "nueva" serie corregida que se presenta en la Tabla 1: (a) Espectro de poder de las dos series, (b) coherencia, (c) fase.

For example, the seasonal pattern is very similar (Fig. 2), as are the major interannual features in the two series (Fig 3). Both series indicate seasonal maxima in alongshore stress during austral winter (peak in September) and minima in summer (lowest in January). Both series show increases in alongshore stress associated with El Niño episodes and some indication of a general linear upward trend from the mid-1950s to 1982-83.

For readers who may be more comfortable with correlation coefficients than with coherence spectra, regressing the "old" series on the "new" series yields a correlation of r = .975 and a regression line slope of b = 1.14. Transforming the two series to "anomalies", by subtracting the

Fig. 2. Seasonal pattern (long term 1953-84 mean monthly values) of the "old" monthly series of alongshore component of wind stress reported by Bakun (1987) and of the "new" corrected series presented in Table 1.

Fig. 2. Patrón estacional (promedios mensuales a largo plazo 1953-84) de la serie "antigua" de la componente del esfuerzo del viento a lo largo de la costa reportada por Bakun (1987) y la "nueva" serie corregida presentada en la Tabla 1.



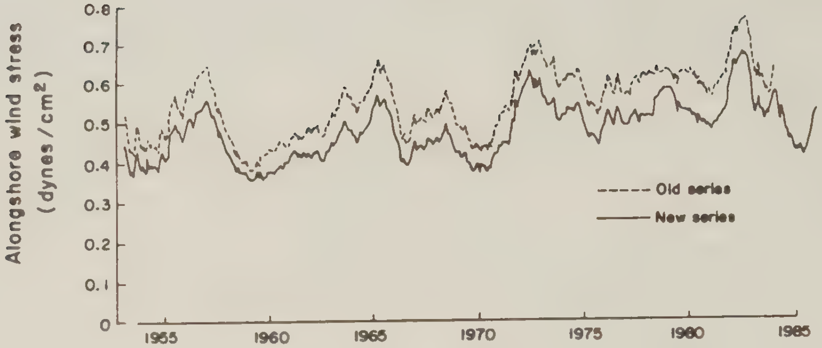


Fig. 3. Low-frequency nonseasonal variations: 12-month running means of monthly time series values of the "old" monthly series (dashed line) of alongshore component of wind stress reported by Bakun (1987) and the "new" corrected series (solid line) presented in Table 1.

Fig. 3. Variaciones de baja frecuencia no estacionales: promedios moviles de 12 meses de los valores de la "antigua" serie mensual (línea punteada) de la componente del esfuerzo del viento a lo largo de la costa, reportada por Bakun (1987) y la "nueva" serie corregida (línea solida) presentada en la Tabla 1.

appropriate 1953-84 long term monthly mean from each monthly value, yields r = .962 and b = 1.12. Removing the seasonal variation and the long term linear trend by "12th-differencing" each series (subtracting from each value the value for the same month one year earlier) yields r = .953 and b = 1.09. The regression line directly intersects the origin (intercept = 0.00) in all three cases.

Bohle-Carbonell (this volume), in examining the fractal dimensions of several series related to the anchoveta fisheries, uses the Bakun (1987) series. As discussed in Mendelssohn (this vol.), there is a close relationship between fractal dimension and fractal differencing in time series. Statistical estimates of the fractional differencing parameter *d* are determined from properties of the observed and theoretical spectrum. As the "old" and "new" series have similar spectra, there should be little change in these estimates, and the use of the "new" series should not affect Bohle-Carbonell's conclusions. (In fact, the estimate of fractional differencing for the "old" series is *d = .2212,* while for the "new" series it is *d = .2857,* see Mendelssohn (this vol.) for details).

Cury and Roy (1989) estimate optimal environmental windows for the Peruvian anchoveta, as well as for species from other eastern boundary current regions, using a turbulence index (wind speed cubed) as the environmental variable. Their study is unaffected by this correction, as they use the Trujillo series of Mendo et al. (1987). It is expected that other studies that may have used the earlier series will be similarly unaffected to any substantial degree.

References

Bakun, A. 1985. Comparative studies and the recruitment problem: searching for generalizations. CalCOFI Rep. 26: 30-40.

Bakun, A. 1987. Monthly variability in the ocean habitat off Peru as deduced from maritime observations, 1953-84, p. 46-74. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Bakun, A. and R.H. Parrish. 1980. Environmental inputs to fishery population models for eastern boundary current regions, p. 67-104. *In* G.D. Sharp (ed.) Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, Lima, Peru, 20 April-5 May 1980. IOC Workshop Rep. 28. UNESCO, Paris. 323 p.

Bakun, A. and R.H. Parrish. 1982. Turbulence, transport, and pelagic fish in the California and Peru Current systems. CalCOFI Rep. 23: 99-112.

Cury, P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Can. J. Fish. Aquat. Sci. 46(4): 670-680.

Mendo, J., L. Pizarro and S. Castillo. 1987. Monthly turbulence and Ekman transport indexes, 1953 to 1985, based on local wind records from Trujillo and Callao, Peru. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Shepherd, J.G., J.G. Pope and R.D. Cousens. 1984. Variations in fish stocks and hypotheses concerning their links with climate. Rapp. P.-v. Réun. CIEM 185: 255-267.

EDUCATIONAL CAMPAIGN IN TURKEY: ONLY THE BEGINNING

Dogal Hayati Koruma Dernegi (DHKD), The Society for the Protection of Wildlife in Turkey, is organizing a large scale campaign to educate visitors to the Iztuzu beach at Dalyan and the local people on the importance of this beach for nesting loggerhead sea turtles, Caretta caretta. Special protection measures are now accurately carried out by the Directorate for Specially Protected Areas, headed by Tunca Toskay. DHKD, in cooperation with a German conservation organisation which is especially interested in the protection of sea turtles, Aktion Gemeinschaft Artenschutz (AGA), will explain to the foreign and Turkish visitors to the beach why the protection measures are taken and what the visitors can do to help the conservation of the threatened sea turtles. Special information centers have been established on the beach and in Dalyan village, where visitors can watch videos on turtles and receive informative leaflets. The well known graphic designer Sadik Karamustafa designed a set of five postcards that is available in Turkish and English; Karamustafa received tow prestigious art awards for these designs. Furthermore, a large poster is available in Turkish and English which depicts a sea turtle asking the reader: "I am here since 95,000,000 years, and you?" Brochures in three languages are handed to tourists with a request not to camp in the area, not to set up umbrellas, not to leave litter, etc.

DHKD president Nergis Yazgan says: "This is not an end but only the beginning. The good example of Dalyan, in which concern for the conservation of an ecologically important area outrode a huge touristic development plan, leading to the annulation of the whole project, we believe, will set a positive model for many areas in many countries." DHKD is aiming towards something much more ambitious: with the approval and collaboration of the Turkish government and together with World Wildlife Fund (WWF), they want a General Coastal Management Plan for the whole Turkish south coast. DHKD President Nergis Yazgan: "... otherwise piecemeal and unplanned development will ruin the whole Turkish south coast."

For more information, please contact **DHKD**, PK 18, 80810 Bebek, Istanbul, TURKEY. Phone +9011636324 FAX +9011630582.

NEW INITIATIVES TO STUDY SEA TURTLES IN THE EASTERN PACIFIC

Although numerous studies have been underway for some time at sea turtle nesting sites in the eastern Pacific, research on sea turtles in marine habitats of this region has been relatively scarce and not widely known. For example, an important body of data covering historical and current sightings, strandings, and incidental and intentional captures of turtles in the northeastern Pacific (north of 29°45'N) was compiled by Margie Stinson (1984). Her findings show that the leatherback is the most frequently encountered turtle in the area, followed by green, loggerhead and olive ridley sea turtles. Stinson's work also included tagging and monitoring a small aggregation of green turtles in San Diego Bay, near the warmwater discharge of a power plant. At present, Donna McDonald and Peter Dutton (Sea World Research Institute, San Diego) are in the process of expanding upon the work Stinson initiated in San Diego Bay. They will attempt to identify the origins and migratory habits of the turtles, while also looking into the possible influence of various pollutants known to occur in high levels within the Bay. With the help of McDonald, Dutton and others, turtle strandings in California are now being officially responded to and compiled by Joe Cordaro of the National Marine Fisheries Service (NMFS) at Terminal Island, California (tel: 213-514-6196).

Another little known but important research effort has been underway in the eastern tropical Pacific by Bob Pitman (NMFS, Southwest Fisheries Center [SWFC], La Jolla, California). For several years now, on his own initiative, Pitman has been compiling sightings of turtle he has made in pelagic habitats while working on NOAA/NMFS vessels monitoring porpoise stocks in the region. Preliminary distributional maps of his findings have appeared in SWFC reports (most recently, Lierheimer et al., 1989a, 1989b). The full results of this work are currently being prepared for publication by Pitman, in collaboration with Dr. Aleta Hohn (NMFS SWFC). Pitman's work has already provided the basis for an expanded effort whereby he and Ms. Sallie Beavers (NMFS SWFC) plan to opportunistically capture, measure, tag, and collect blood samples and stomach contents from turtles encountered on the high seas. Satellite telemetry is planned (in cooperation with the U.S. Fish and Wildlife Service), and Dave Owens' research group at Texas A&M University has also been assisting Beavers and Pitman in these endeavors. Project activities off Baja California (Mexico) and in other waters within 200 miles of Mexico will proceed in cooperation with Mexican sea turtle biologists, including René Marquez.

Considerable interest exists in the reports of large concentrations of immature loggerheads off Baja California, since loggerheads are not known to nest to any extent in the eastern Pacific. Pitman has sighted and photographed these loggerheads, and Grant Bartlett (1989) has published a fascinating report of this phenomenon, based mainly on interviews with Mexican informants. According to Pitman, the turtles occur in an area rich with the pelagic red crab, Pleuroncodes planipes, a likely food source. The possibility exists that the loggerheads may be part of a population that nests in southern Japan. Some support for this idea has been provided by Uchida and Teruya (1988), who report the recovery of a tagged loggerhead 75 km off San Diego (32°39'N, 117°58'W) that had been released from a head start project 2.3 years earlier near Okinawa. The turtle was found entangled and dead in a drift gill net by Christopher Golden, a fisherman and graduate student at Humboldt State University, California. A second untagged turtle was also found in the net, and 12-15 others were seen in the vicinity the following day. Of related interest is the recent recovery of a 23 cm loggerhead found dead in a scrap of gill net far north of the Hawaiian Islands (39°N, 165°W) (NMFS unpubl. data). This finding is consistent with the transpacific movement for young loggerheads proposed by Uchida and Teruya (1988).

Another new project complementing the work of Beavers and Pitman is a planned NMFS shipboard observer program to record turtles incidentally caught by U.S. tuna purse seiners in the eastern Pacific. Preliminary reports from the mid-1970's suggest that the take of turtles and resulting mortality in this fishery is low. However, more current information is needed to ensure a sound plan for conservation. The tagging, measuring, and release of live turtles captured by purse seiners may also be possible in this observer program.

Lastly, the recent "migration" and residency of Drs. Scott and Karen Eckert (MTN Editors) to southern California will surely result in new and exciting work on turtles in the eastern Pacific.

As a SWFC researcher based in Honolulu, my own interest in sea turtles of the eastern Pacific arises from several factors. For one thing, the leatherbacks, olive ridleys, and possibly some of the green turtles found in Hawaiian waters may very well originate from this region. In addition, this past January I had the opportunity to spend three days visiting coastal sites in southern California where turtles are sometimes seen or have stranded, such as near Encina power plant at Carlsbad and the San Babriel River in Long Beach. This reconnaissance was made possible with support from the California Academy of Sciences in San Francisco, where I had been invited to speak about sea turtles to the membership. I have also been intrigued for years by the narratives of shipwreck victims who, while adrift in the eastern Pacific, have frequently encountered turtles and used them for food to survive (Robertson, 1973; Bailey and Bailey, 1974). These fascinating accounts are required reading for anyone interested in unraveling the mysteries of turtles in their pelagic habitats.

Significant opportunities clearly exist to learn more about the lives of turtles at sea in the eastern Pacific. During the coming years, conservation efforts are sure to benefit from the research initiatives taking hold at this time.

Bailey, M. and Bailey, M. 1974. Staying alive! Ballantine Books, New York, 129p.

Bartlett, G. 1989. Juvenile Caretta off the Pacific coast of Baja California. Noticias Caguamas 2:2-10.

Lierheimer, L. J., Fielder, P. C., Reilly, S. B., Pitman, R. L., Ballance, L. T., Thomas, G. G. and Behringer, D. W. 1989a. Report of ecosystem studies conducted during the 1988 eastern tropical Pacific dolphin survey on the research vessel *David Starr Jordan*. NOAA Tech. Memo. NMFS-TM-NMFS-SWFC-131, 125p.

Lierheimer, L. J., Fielder, P. C., Reilly, S. B., Pitman, R. L., Ballance, L. T. and Behringer, D. W. 1989b. Report of ecosystem studies conducted during the 1988 eastern tropical Pacific dolphin survey on the research vessel *McArthur*. NOAA Tech. Memo. NMFS-TM-NMFS-SWFC-132, 121p.

Robertson, D. 1973. Survive the savage sea. Bantam Books, New York, 249p.

Stinson, M. L. 1984. Biology of sea turtles in San Diego Bay, California, and the northeastern Pacific Ocean. Master's thesis, San Diego State University, San Diego, 578p.

Uchida, S. and Teruya, H. 1988. Transpacific migration of a tagged loggerhead, Caretta caretta. Intl. Symp. Sea Turtles, Hiwasa, Japan. Poster presentation.

GEORGE H. BALAZS, Southwest Fisheries Center Honolulu Laboratory, NOAA National Marine Fisheries Service, 2570 Dole Street, Honolulu, HAWAII 96822-2396 USA.

An Assessment Of The Pacific Swordfish Resource

Norman W. Bartoo and Atilio L. Coan, Jr.

The swordfish *(Xiphias gladius)* is cosmopolitan in its distribution, found in all tropical to temperate oceans. In the Pacific Ocean, swordfish are generally distributed from Asia to the Americas and from 50 degrees north to 50 degrees south latitude. Swordfish are taken by many countries with various gears. For a complete discussion of Pacific swordfish fisheries and their trends the reader is referred to Sakagawa (this volume). These fisheries are both coastal and high-seas in nature. Data available from these fisheries provide the basic information from which to draw inferences about the state of the swordfish stocks, in this chapter the condition of the Pacific swordfish resource.

We have chosen two stock structure hypotheses which are consistent with previous reviews of the condition of the resource (Sakagawa and Bell 1980). One hypothesis envisions a single Pacific stock, under the rationale that the resource appears to be contiguous, with zones of local high catches due to high abundance or high vulnerability, and the assumption that the population is sufficiently mobile to make the concept of local depletion on an annual basis a non-issue. Our second hypothesis is to separate out 3 general areas of apparent high abundance in the northwest, southwest and east Pacific, made contiguous by a broad region of lower catches.

Data and Rationale

Each country and fishery reports different data ranging from estimated total catch to detailed catch and effort by area. A review of all available Pacific swordfish data indicates that only the Japanese longline fishery data are suitable in their detail and time period covered to provide a basis for a catch-per-unit-effort (CPUE) assessment of the Pacific swordfish stock. This conclusion was reached by others who previously investigated the swordfish resource (Sakagawa and Bell 1980, Shomura 1980). The available longline data contain both catch in numbers and nominal hooks fished by 5 × 5 degree squares and by month. These data can provide a measure of CPUE for a useful time series. The absence of reliable size sample data (length-frequency or weight-frequency) for the time series precludes the use of age-structured assessment techniques such as cohort analysis for the stock structures assumed.

Total Catch

Table 1 shows Pacific swordfish catches in weight by country. Figure 1 shows both the Japanese longline catch and the estimated Pacific total catch in weight. The Japanese longline catch represents a large proportion of the annual catches throughout the time series. Note from Table 1 that estimates of catch for many countries are available only for the second half of the time series. As a result, the total catch for the first half of the time series is underestimated by an unknown but presumably significant amount. These catch estimates are from the FAO (1971-1987) and published and private sources within various countries. After 1970, when all countries shown in Table 1 are represented, the Japanese longline catch has maintained a relatively constant and high proportion of the total catch.

Catch and Effort

The Japanese catch-and-effort series of data, 1952 to 1980 (Fisheries Agency of Japan 1965-1982, Agricultural Resource Agency of Japan 1953-1964), have changed within the time series, due mostly to substantial changes in the way the fishery is operated (Shomura 1980, Sakagawa et al in press, Ueyanagi 1974). During

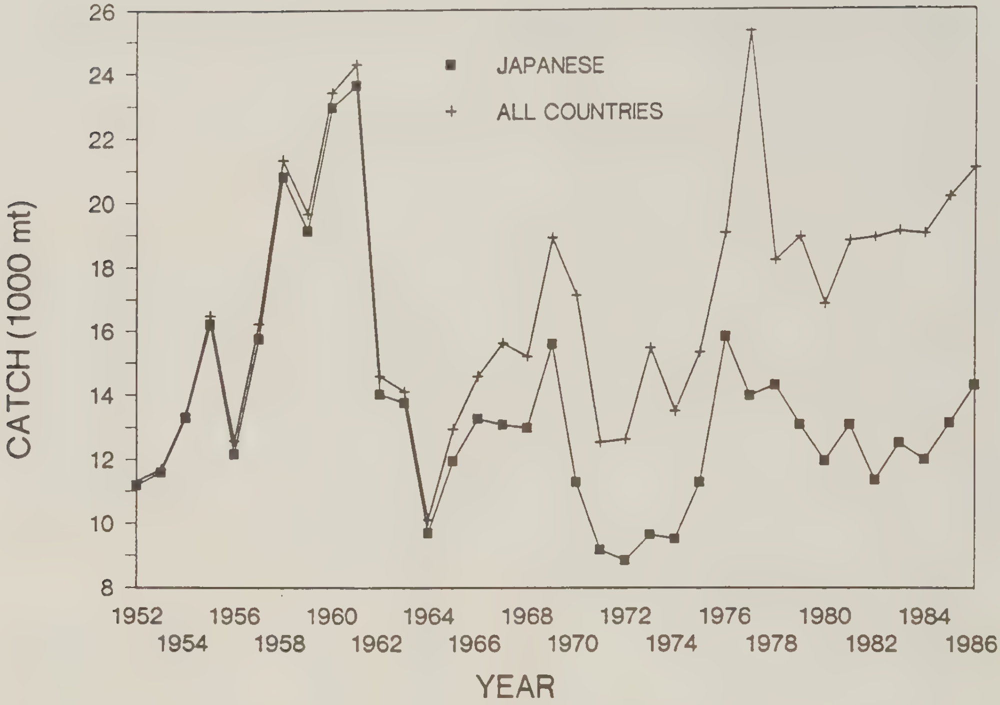


Figure 1. Japanese longline catch and the estimated catch of all countries fishing for swordfish in the Pacific Ocean.

the period 1952 through about 1962, swordfish were specifically targeted in some areas by fishing at night with squid for bait. The fishery changed substantially in the early 1960s (approximately 1962 — 1964). Day operations with mixed bait types became the norm, which has continued to the present. The strategy of Japanese longlining tuna changed at about this same time, de-emphasizing albacore *(Thunnus alalunga)* and emphasizing sashimi grade tunas (Sakagawa et al in press), mostly bigeye tuna *(T. obesus)*, bluefin *(T. thynnus)*, and yellowfin *(T. albacares)*. Thus, the data series is broken in two in the early 1960s. To further complicate matters, portions of the fleet began "deep longlining" in 1974 to increase the catch rate on bigeye tuna (Suzuki and Warashina 1977). The effect was that the CPUE of the deep longline operations was about 80% as efficient as the standard operations for albacore, swordfish, and yellowfin tuna. The different operations are not distinguished in the published data, and therefore cannot be compensated for in the calculations without additional information, but must instead by considered qualitatively in the results.

Previous assessments of Pacific billfish and swordfish in particular have relied on "Honma's method" (Honma 1973, Shiohama 1971) to calculate the portion of the total effort fished in any particular area that is presumed to be effective for the species of interest. Because of the changes in the fishery and qualitative differences in the data with passage of time and the fact that swordfish appear to be a target species in a few areas and a true incidental catch in others, we suspect that the assumptions required to implement Honma's method for swordfish are not fully met. Consequently, we have chosen to use nominal CPUE and a data stratification which allows the separation of target or high catch rate areas from areas where swordfish appear as incidental catches. This procedure is done to account for the spatial distribution of populations, a concept presented by MacCall (1983).

This approach to segmenting or stratifying the population is based on the premise that different portions of the population may react differently to exploitation and should be examined independently. An example of different reactions expected might include a shrinking of the areal distribution and decline in CPUE of low density areas as the stock is reduced and the remaining population continues to concentrate itself in higher density areas. Fortunately, this approach appears robust with respect to strata chosen, as our analysis was unaffected by several different choices of strata. We have chosen three strata, a high density or CPUE stratum (target areas), a low density or CPUE stratum (incidental catch areas), and an intermediate or buffer stratum. The primary purpose of the latter is to separate the signals from high and low CPUE strata by minimizing the subjectivity in defining the high and low strata.

Stratification

The annual distribution of catch in numbers by 5 × 5 degree square shows 3 areas or regions of concentrated catches. These 3, northwest (N.W.), east (E), and southwest (S.W.) Pacific, appear year after year in the data series. Figure 2 shows the catch distributions for 4 years chosen throughout the time series. Of interest is the fact that the exact squares producing high catches may shift slightly from year to year. This presumably mirrors the shift in fish distribution caused by environmental or oceanographic changes, etc. A great portion of the area fished

Table 1. Pacific Ocean catches (metric tons) of swordfish

YEAR	JAPAN	TAIWAN	KOREA	USA	CHILE	PERU	PHIL	OTHERS	TOTAL
1952	11182			157					11339
1953	11604			85					11689
1954	13301	77		14					13392
1955	16220	185		80					16485
1956	12167	254		163					12584
1957	15771	250		222					16243
1958	20815	247		279					21341
1959	19136	262		265					19663
1960	22944	273		192					23409
1961	23636	432		218					24286
1962	14037	544		23					14604
1963	13775	300		58					14133
1964	9703	300		109					10112
1965	11955	300		194	200	300			12949
1966	13283	600	41	277	200	200			14601
1967	13083	838	47	181	200	1300			15649
1968	12983	974	55	118	200	800		100	15230
1969	15612	1023	89	610	300	1200		100	18934
1970	11301	1053	115	558	200	2400	1400	100	17127
1971	9182	1149	115	91	200	200	1500	100	12537
1972	8846	1111	115	157	100	600	1600	100	12629
1973	9644	1269	115	363	400	1900	1700	100	15491
1974	9517	1157	115	383	218	270	1848	3	13511
1975	11274	1099	115	510	218	158	1976		15350
1976	15843	856	444	49	13	295	1558		19058
1977	13997	8197	265	301	32	420	2103		25315
1978	14333	779	198	1536	56	436	890		18228
1979	13091	1060	365	346	40	188	3845	7	18942
1980	11953	1459	329	706	104	216	1716	380	16863
1981	13078	909	257	674	294	91	1940	1575	18818
1982	11350	1107	194	989	285	154	3468	1365	18912
1983	12511	1268	135	1534	342	225	2974	120	19109
1984	11986	1387	54	2878	103	298	2277	47	19030
1985	13125	1429	56	3064	342	92	2036	18	20162
1986	14295	1357	37	2131	764	33	2089	350	21056
1987				1580					1580

produces relatively low annual catches of swordfish.

The proportion of swordfish to all tunas and billfish in the total catch in each 5 × 5 degree square (Fig. 3) reveals broad areas of very low representation which generally correspond to areas of low total catch, described above, and appear to be indicative of incidental catch areas. Squares with a high proportion of swordfish in the catch correspond with areas of higher catches.

As stated previously, two stock structure hypotheses are considered. These correspond to the areas described above (Fig. 4) and are approximately the same as those used in previous assessments (Sakagawa and Bell 1980). The exact boundaries chosen are not critical because of the stratification concept employed.

The index of abundance chosen, mentioned previously, is nominal annual CPUE in numbers of fish per 10,000 hooks fished for each 5 × 5 degree square. To separate high abundance or possible target squares from lower abundance squares where swordfish are an incidental catch, the CPUE for all squares in the Pacific receiving effort in a year were combined into 3 strata. The first stratum, "high CPUE," contains 15% of the total squares fished which produced the highest CPUEs. The second stratum, "low CPUE," contains 50% of those squares fished which produced the lowest CPUEs. The third stratum, "middle CPUE," contains those squares which produced the 35% intermediate values between the first and second groups.

The rationale for this accumulation scheme is that high abundance squares — possible swordfish target areas or centers of high concentrations — are sought by the fishery year after year and produce the bulk of the catch. The squares are not fixed in number of spatial location. This circumstance accounts for spatial shifts in the resource, which happen from year to year. A key assumption is that the fishery will shift to an adjacent square as the resource shifts. An examination for year-to-year shifts (Fig. 5) shows these squares to be in the same

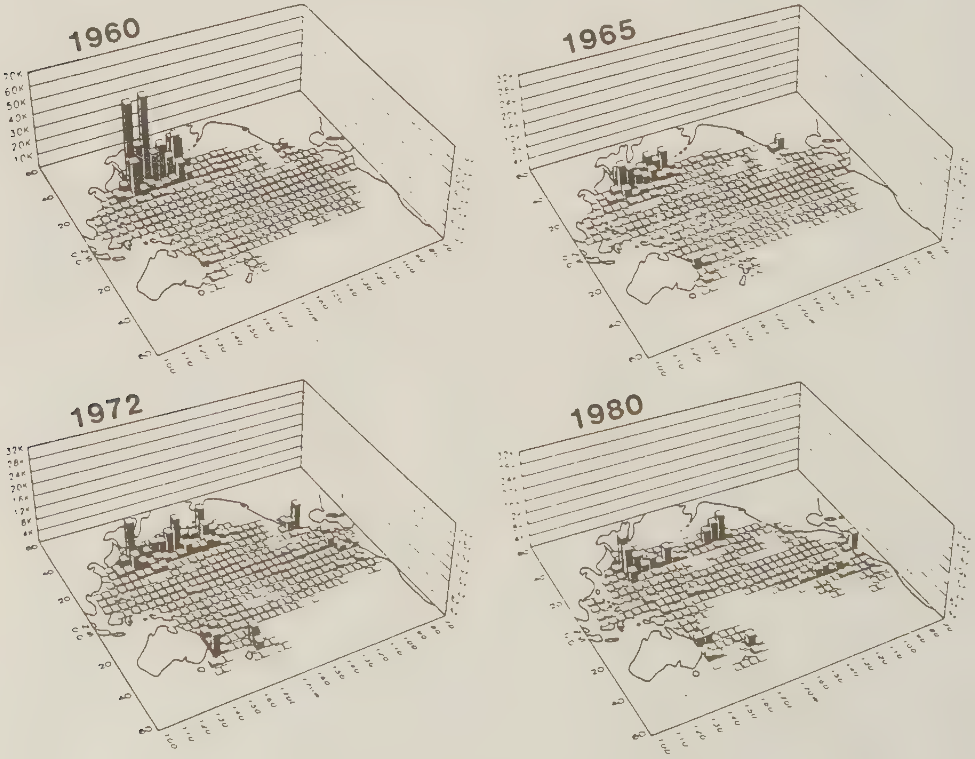


Figure 2. Geographical distribution of Japanese longline swordfish catches in the Pacific Ocean.

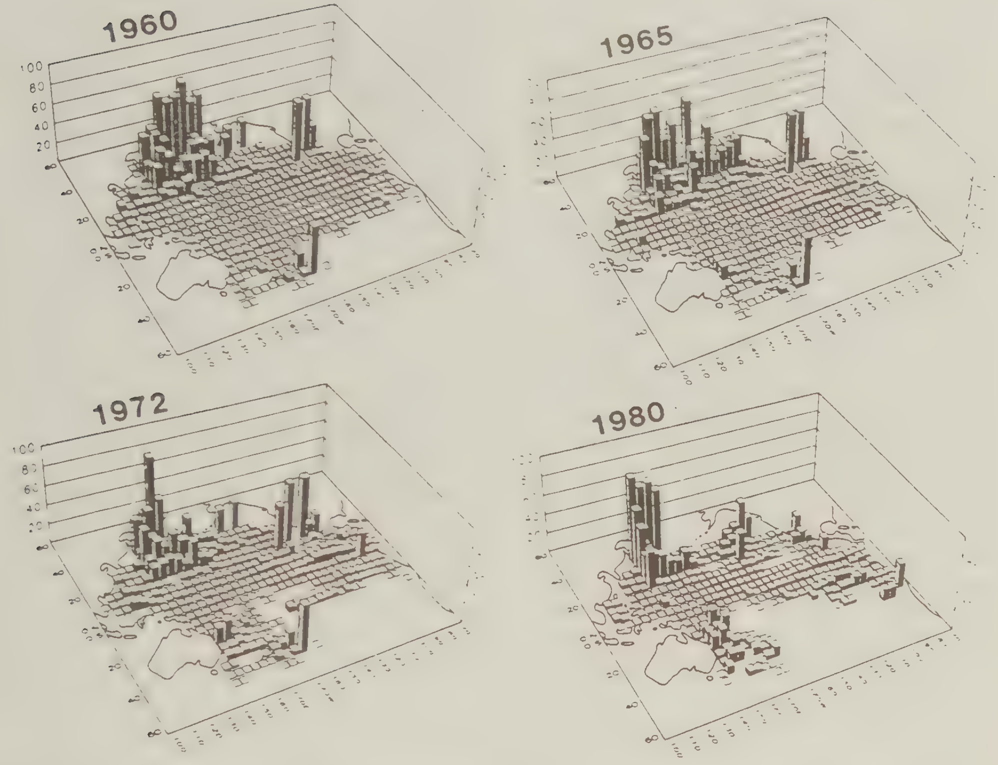


Figure 3. Geographical distribution of Japanese longline percent of swordfish in the total catches of billfishes and tunas in the Pacific Ocean.

general area year after year. The number of squares producing the top catch rates varies for several reasons. The total number of squares fished in the Pacific (Fig. 6) and the concentration of fish, or vulnerability, in each square throughout the entire Ocean varies from year to year. Interestingly, the actual number of squares included in the top catch-rate group each year is remarkably stable. The use of an annual CPUE value removes the effect of seasonality from the data. Although the procedure does lower peak CPUE values, it is consistent throughout the time series.

The stratum of the low catch-rate squares (lower 50%) captures broad areas of the Pacific, mostly contiguous, where low catches, low proportion of swordfish in the overall catch, and low catch rates make swordfish an incidental catch. Figure 7 shows the distribution of these squares for several example years. Figure 6 shows the number of squares contained in the grouping over the time series.

The last stratum of squares, those with the middle 35% of the catch rates, serves two functions. First, it captures into a relatively narrow group those squares where it is uncertain whether swordfish are a target. Second, and more importantly, it serves as buffer separating the high and low catch-rate groups. This buffering obviates the requirement to define precisely the strata where "target" fisheries begin and end. We need only be concerned that the high CPUE stratum has a high enough threshold and that the low CPUE stratum has a low enough one. This condition implies that the CPUE values in the high and low groups will track relative abundance in their designed strata. The benefit is that signals or trends in each extreme have a low probability of becoming confused or distorted by subjective judgment used to separate high CPUE areas from low CPUE areas.

Results and Discussion

Whole Pacific Stock

Figure 8 shows catch over time aggregated by the three CPUE strata. The high CPUE stratum, the top 15%, presents an increasing trend in catch through 1961 and a drop to a lower level in 1962, during the period of changed longline operations described previously. The catch is erratic following the 1962-1964 period, but has stabilized following a few peak catch years in the late 1960s. The other 2 strata, low CPUE and middle CPUE, show relatively smooth, slowly increasing catch trends. Note from Figure 1 that the Japanese longline catch is a relatively constant proportion of the total catch after 1970, when catch estimates became available for most countries.

Figure 9 presents total effort over time for the 3 strata. Effort in the middle and low CPUE strata shows a continuously increasing trend. Effort in the high CPUE stratum approximately follows the pattern of catches.

Figure 10 presents CPUE for the 3 strata for the Pacific-wide case. CPUE in the high stratum shows a slight increasing trend through the early 1960s, a drop to a new plateau following the longline operational changes in the early 1960s, and a stable almost level trend through 1980. This pattern is similar in pattern to that seen in the previous analysis reported by Sakagawa and Bell (1980). Note that effort in the last few years is approximately the same as in the late 1950s, although longline catch and CPUE are lower. This can indicate lower abundance or a reduction in catchability in the later period. Given the operational changes reported, and the relative stability in CPUE in the two periods, the latter explanation seems more plausible. The increase in reported total catch (Fig. 1) since the mid-1970s, however, may have depressed the longline CPUE somewhat. The absence of available longline data for the more recent years precludes further examination.

CPUE trends for the middle and low CPUE

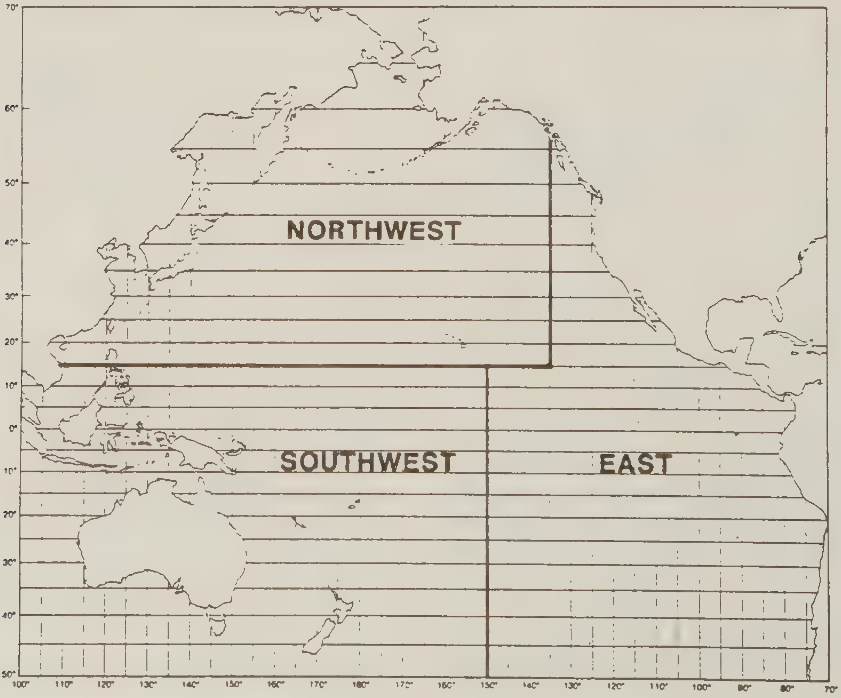


Figure 4. Geographical regions of the Pacific Ocean used as hypothesized stock boundaries.

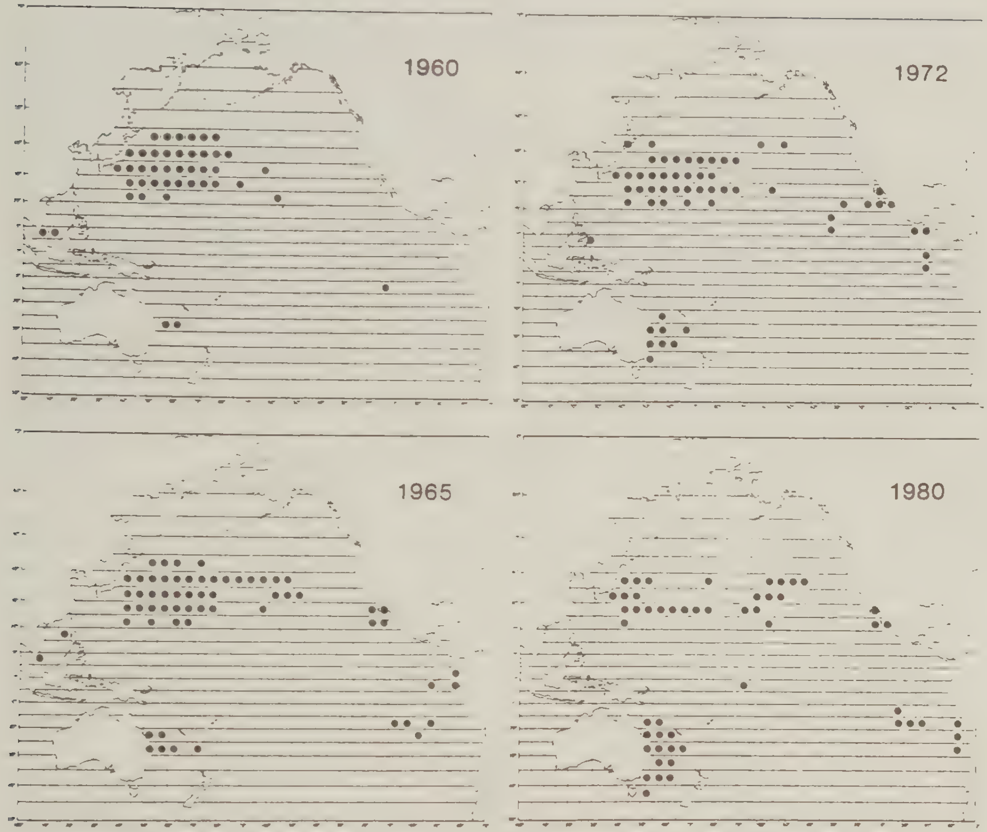


Figure 5. Geographical distribution of 15% of the squares fished by the Japanese longline fishery in the Pacific Ocean that produced the highest CPUEs annually for swordfish.

strata are quite stable and nearly constant, particularly since the mid 1960s. The stable CPUE trends and slowly increasing catch trends are complemented by an increasing trend in effort and does not indicate a decrease in relative abundance over the time series. The large absolute difference in CPUE values between the low CPUE stratum and the high CPUE stratum suggests that swordfish abundance in the lower strata is either considerably lower or that catchability of swordfish in the low CPUE stratum is lower, due to the operational characteristics of the gear. As mentioned preceding, Suzuki and Warashina (1977) indicated that deep longlining techniques used in much of the area covered by the low CPUE stratum reduced catchability of swordfish by approximately 25%. Thus, the effects of deep longlining may affect CPUE values to an unknown degree. If deep longlining effort has increased in proportion to regular effort between 1974 and 1977, as was indicated by Suzuki and Warashina (1977), then catchability of swordfish should be reduced for the deep effort and calculated CPUE will be biased low for the years after 1974. Unavailability of data after 1980 precludes confirmation.

The distribution of squares, or area occupied by the stock in the low CPUE stratum, shows no signs of declining over the time series. The percentage of total squares fished annually from 1960 through 1980 which produced no swordfish is rather stable, ranging from 7% to 13% with most observations at 9%. Any changes in the distributions of catch appear to be due to the complete elimination of effort from areas in the south-central Pacific near island states which produce mostly tropical tunas.

Three-Stock Case

The designation of the 3 stocks or fishery areas shown in Figure 4 was guided by the criterion that the purpose of this stratification is to be able to examine the trends in the high CPUE stratum, described previously, independent of influences of the high catch-rate squares in other areas. This can be useful if swordfish tend to remain in each of the 3 areas after recruitment, thus making location reductions in abundance a possible issue. .As mentioned previously, the actual boundaries chosen are arbitrary because there are no firm, documented critieria available. While it is valid, therefore, to compare CPUE trends for the high catch-rate strata between areas which are isolated, it is not valid to compare CPUE trends for the middle and low catch-rate strata because CPUE values and trends can be biased by the choice of area or stock boundaries. It appears more reasonable to use the whole Pacific case as the abundance trend for the incidental catch areas.

The distribution of the 15% of the 5 × 5 degree squares fished each year having the highest CPUEs in the 3 areas in the Pacific is shown in Figure 11. In the northwest area (N.W.), the number of squares rapidly peaks in 1963 and then declines. From 1969 through 1980, the number of squares shows no strong trend, with about 30 squares per year. In contrast, the number of squares in the eastern area (E) shows an increase from 1963 through the early 1970s. The trend has been level since then, at about 10 squares per year. In the southwest area (S.W.), the number of contributing squares has remained small but has increased over the time series to approximately 10.

Figure 12 shows the catch over time from the 3 years. In the early years, the N.W. area contributed the vast majority. Following the fleet changes in the 1960s, the S.W. and E areas contributed greater amounts to the longline catch.

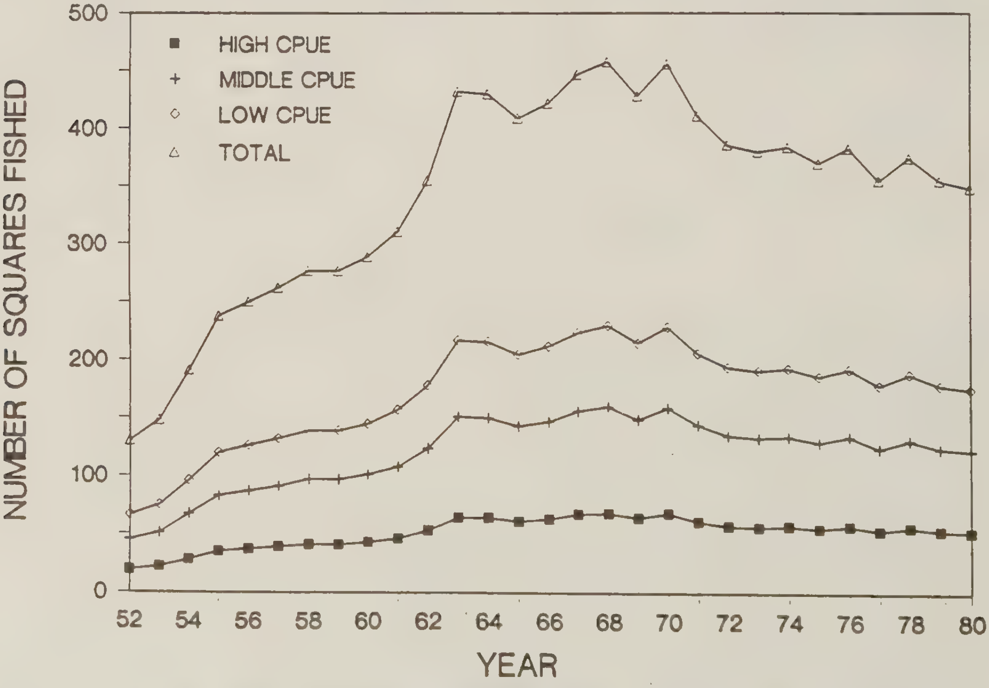


Figure 6. Total number of squares fished annually by the Japanese longline fishery in the Pacific Ocean for three CPUE strata: the top 15% of the squares fished producing the highest CPUEs (HIGH CPUE), the next 35% of the squares fished producing the middle CPUEs (MIDDLE CPUE), and the last 50% of the squares fished producing the lowest CPUEs (LOW CPUE).

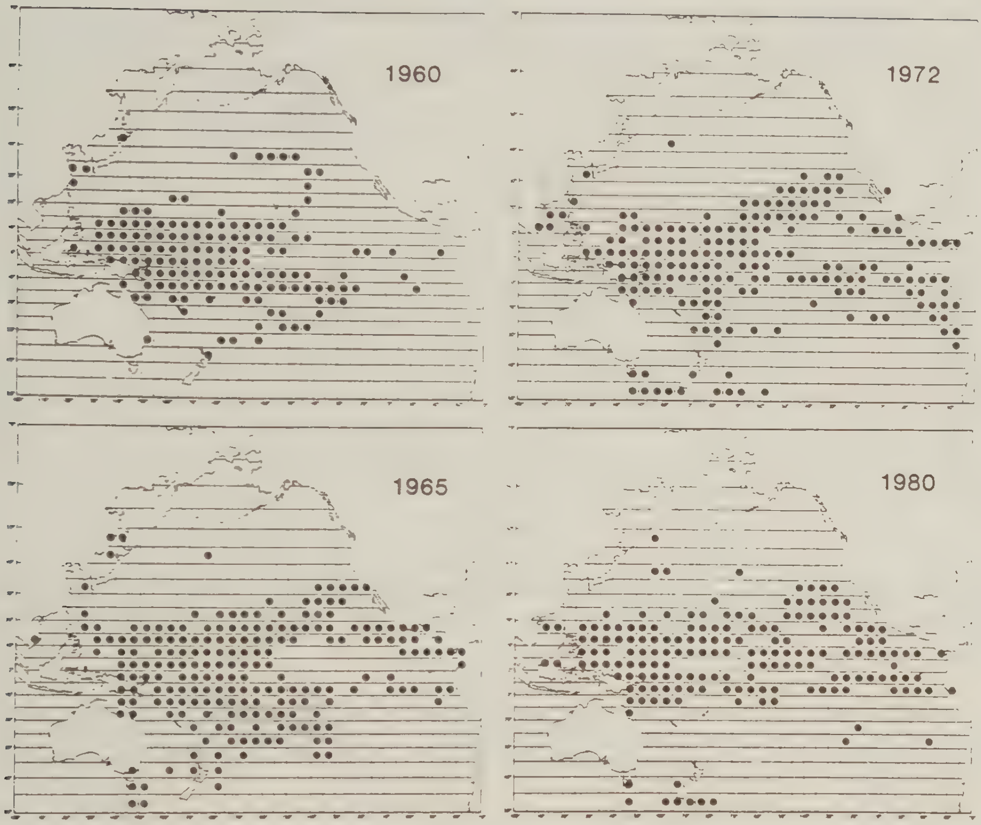


Figure 7. Geographical distribution of 50% of the squares fished by the Japanese longline fishery in the Pacific Ocean that produced the lowest CPUEs annually for swordfish.

CPUE trends for the 3 areas are shown in Figure 13. The pattern in the N.W. is similar to the pattern for the whole Pacific. This similarity is due to the fact that the N.W. area contributes the majority of the catch. The trend in CPUE for E area has been constant or level since the late 1960s, although some of the peak CPUEs are greater than in the rest of the Pacific. This situation also prevailed for the S.W. Pacific. The CPUE trends in the 3 areas in recent years are flat and do not indicate a change in the resource.

Conclusions

The analysis and examination of data leads us to several conclusions, some of which are not qualitatively different than those from previous examinations.

Data for swordfish have changed little since the last Pacific-wide look at swordfish. Many of the data are generally not adequate for assessment purposes, the notable exception being the Japanese longline fishery data through 1980. Total estimated catches in weight appear to be at about the same general level seen in the late 1950s; however, there appears to be incomplete reporting of catches in years prior to the mid-1960s. The historical catch-and-effort data for the Japanese longline fleet were affected by major changes in both the operation of the gear — reduction in night sets and bait changes, and in the strategy of fishing operations — changing from albacore to tunas for the internal Japanese sashimi market.

Swordfish appears to be a target or very important species in at least 3 areas of the Pacific,

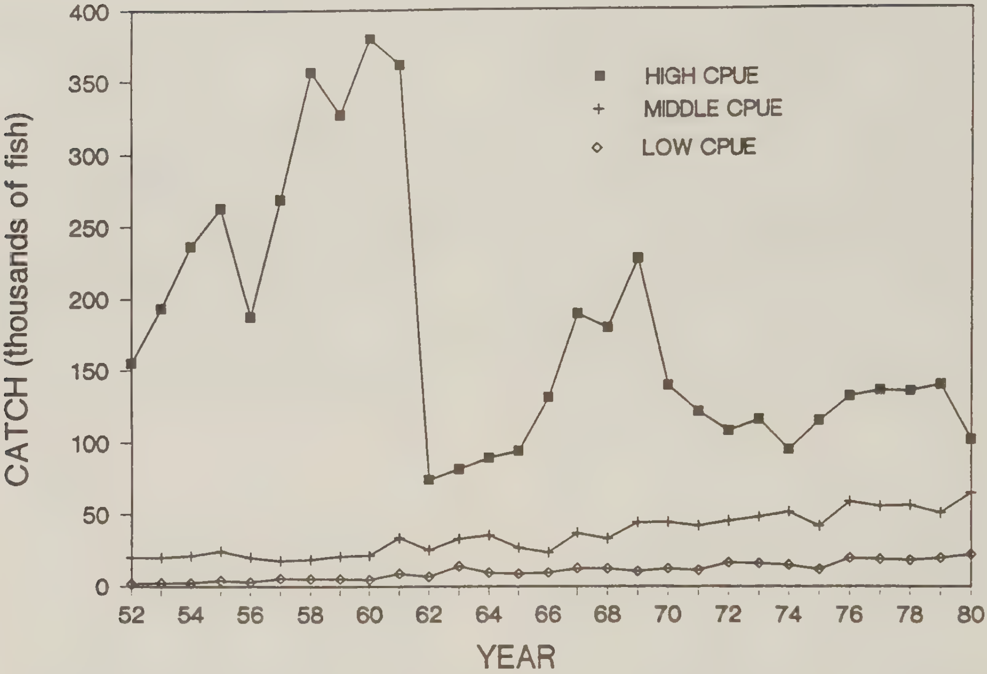


Figure 8. Annual Pacific Ocean swordfish catches from the Japanese longline fishery in three CPUE strata: the top 15% of the squares fished producing the highest CPUEs (HIGH CPUE), the next 35% fo the squares fished producing the middle CPUEs (MIDDLE CPUE), and the last 50% of the squares fished producing the lowest CPUEs (LOW CPUE).

the northwest, east, and southwest. Consistently, year to year, high catch and CPUE areas are fished in each area. Additionally, swordfish appear to be an incidental catch taken in relatively small numbers in a broad contiguous area of the Pacific associated with tropical tuna operations.

When considered as a single, Pacific-wide stock with several high catch-rate areas, the CPUE in the target areas showed a slowly increasing trend through the early 1960s. In the early 1960s, CPUE values dropped by about ⅓ and have remained about the same since. The drop in CPUE coincides with the change in longling operations. The CPUE trend in the area where swordfish are an incidental catch is stable, slowly increasing throughout the time series. The change in operations is not seen in this data series.

If considered as 3 stocks, the northwest stock high catch-rate stratum follows the same CPUE pattern as the total-stock case, mostly because the N.W. stock provides the bulk of the catch. In the eastern stock, CPUE has shown considerable highs and lows since the late 1960s, but the trend is level and this stock yields about ⅕ the catch of the N.W. stock. The southwestern stock also yields about ⅕ that of the N.W. stock and has shown an erratic but level trend in CPUE since 1970. In all 3 areas, the actual CPUE values are similar, with the S.W. area tending to be slightly higher.

The effects of those fisheries with increased reported catches in the latter half of that time series, such as the U.S.A., Peru, and Philippines, is unknown. The longline catches used, however, are based on approximately the same reporting rate throughout the time series and should not be affected by the changes in reporting rates. The CPUE indices developed here show no declining trends. Nothing definitive can be said about yield-per-recruit realized by the various fisheries or about optimum size for capture due to the lack of published size data. As a cursory measure, we note that weight per fish in the Japanese longline fishery has been about the same since 1977 (total weight/total catch in numbers).

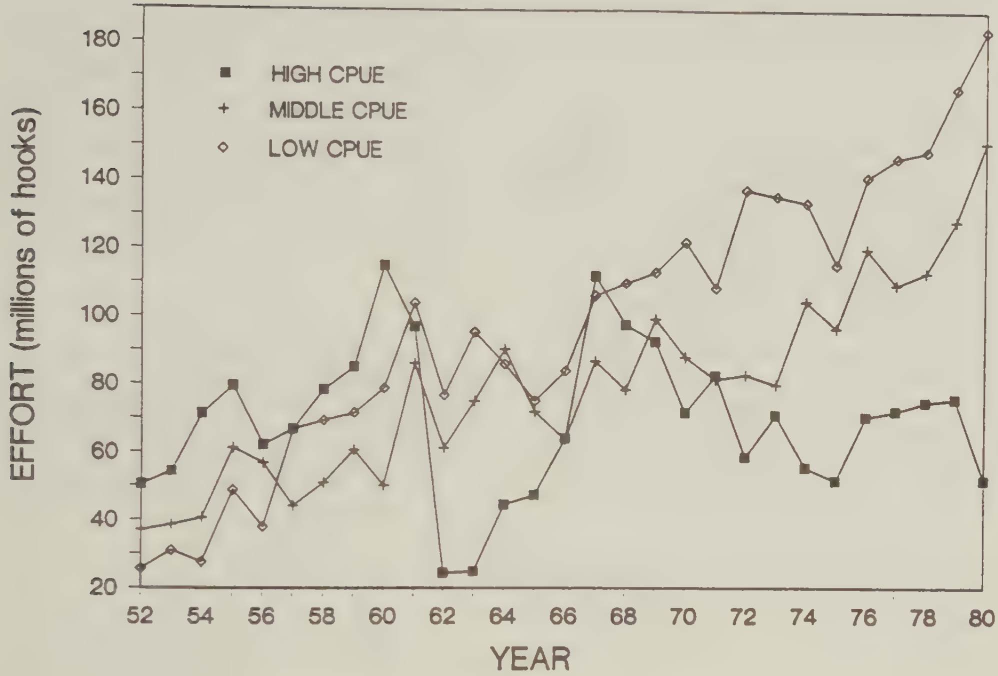


Figure 9. Annual Pacific Ocean hooks fished by the Japanese longline fishery in three CPUE strata: the top 15% of the squares fished producing the highest CPUEs (HIGH CPUE), the next 35% of the squares fished producing the middle CPUEs (MIDDLE CPUE), and the last 50% of the squares fished producing the lowest CPUEs (LOW CPUE).

Based on our examination of the Japanese longline CPUE data, and our interpretation of the changes which occurred in the fishery over time, we conclude that the stocks do not appear to have been exploited heavily enough to cause a declining trend in CPUE and, by extension, in abundance, through 1980. It is actually possible that CPUE may have trended upward slightly since 1974 as the practice of deep longlining increased and estimated CPUE was biased downward, an unknown amount. In an attempt to confirm our conclusions we have examined total swordfish catch and total effort data for the Taiwan and Korean longline fleets. The Taiwan data cover the period 1975 through 1985, with 1980, 1981 and 1982 missing. The Korean data cover the 1975 through 1982 period. The calculated CPUE values for both fleets are very low, less than 1.2 fish per 10,000 hooks. The trend in CPUE is realtively stable, varying between 0.4 and 1.2, similar to that observed for the Japanese fleet's low CPUE stratum over the entire time series (1952 — 1980).

Summary

The Pacific swordfish resource is assessed using catch-per-unit-effort (CPUE) realized by the Japanese longline fleet as an indicator of abundance. Lack of data for other fisheries, and absence of reliable size sample, limits the assessment to CPUE trends and comparisons. A time series of data from 1952 through 1980 is used. This series of data is not consistent throughout due to changes in the fishery and fishing strategy. Attempts to standardize or calculate effective fishing effort are rejected because of changes which occurred in the fishery and because swordfish are, depending on location, both a target species and an incidental catch. Nominal CPUE (numbers of fish caught per 10,000 hooks fished) is used in conjunction with a stratification methodology which separated high catch-rate "target" areas from low catch-rate incidental catch areas. Two stock structure cases were considered: 1. Pacific-wide and 2. three stocks: northwest, east, and southwest.

Results for the whole-Pacific case show that CPUE for target areas increased slowly from

the early 1950s through the early 1960s, then dropped by approximately ⅓ in the 1963 — 1965 period and has remained level since. The change in CPUE levels in the early 1960s corresponds to operational changes in the longline fleet. The CPUE for incidental catch areas shows a very slow long-term increase without the abrupt change noted in the target area CPUE.

Results for the three-stock case show that the CPUE pattern in target areas in the northwest Pacific follows the total-Pacific case because this area produces the bulk of the catch. The CPUE in the east Pacific was very erratic in the early fishery years. Increased effort and operational changes after 1965 reduced some of the CPUE variability and produced a near level trend in CPUE. The CPUE trend in the southwest Pacific is erratic (more so in the earlier years of the fishery) but flat since 1970.

The conclusion reached is that none of the data examined indicates that the stock(s) have been exploited heavily enough to cause a noticeable decline in CPUE through 1980. Sketchy data for Taiwan and Korean longline fleets covering the 1975 to 1985 period show an extension of the Japanese data trends for the low CPUE stratum. The conclusion that no decline is evidenced by data examined may be conservative. The increase in deep longlining since 1974, when corrected for, may possibly elevate CPUE values in the last part of the time series. The inclusion of detailed Japanese data from 1980 — 1988 could be useful in confirming these conclusions.

Acknowledgment

We acknowledge and thank those people who helped prepare the text and figures, including Roy Allen, Lorraine Prescott, Henry Orr, and Ken Raymond. Thanks to our colleagues David Au, Dave Holts, Gary Sakagawa, and James Squire for their reviews and suggestions. Special thanks to Alec MacCall for his help.

Literature Cited

FAO. 1971-1987. Yearbook of fishery statistics, catches and landings 1970-1985. Food and Agriculture Org. of the United Nations, Vol. 30-61.

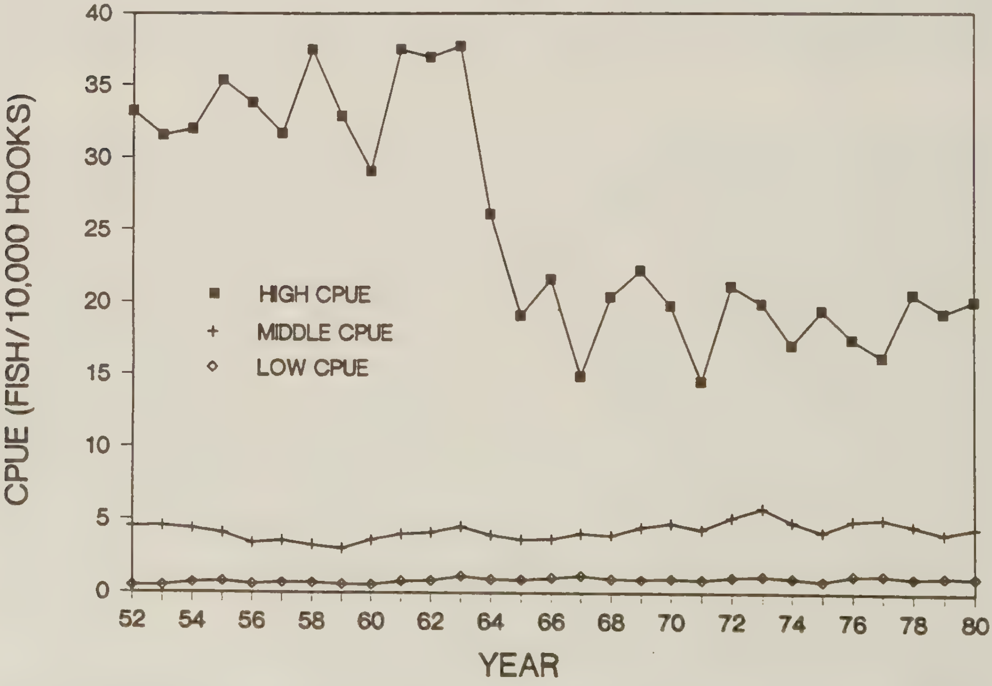


Figure 10. Annual Pacific Ocean catch-per-unit-effort for the Japanese longline fishery in three CPUE strata: the top 15% of the squares fished producing the highest CPUEs (HIGH CPUE), the next 35% of the squares fished producing the middle CPUEs (MIDDLE CPUE), and the last 50% of the squares fished producing the lowest CPUEs (LOW CPUE).

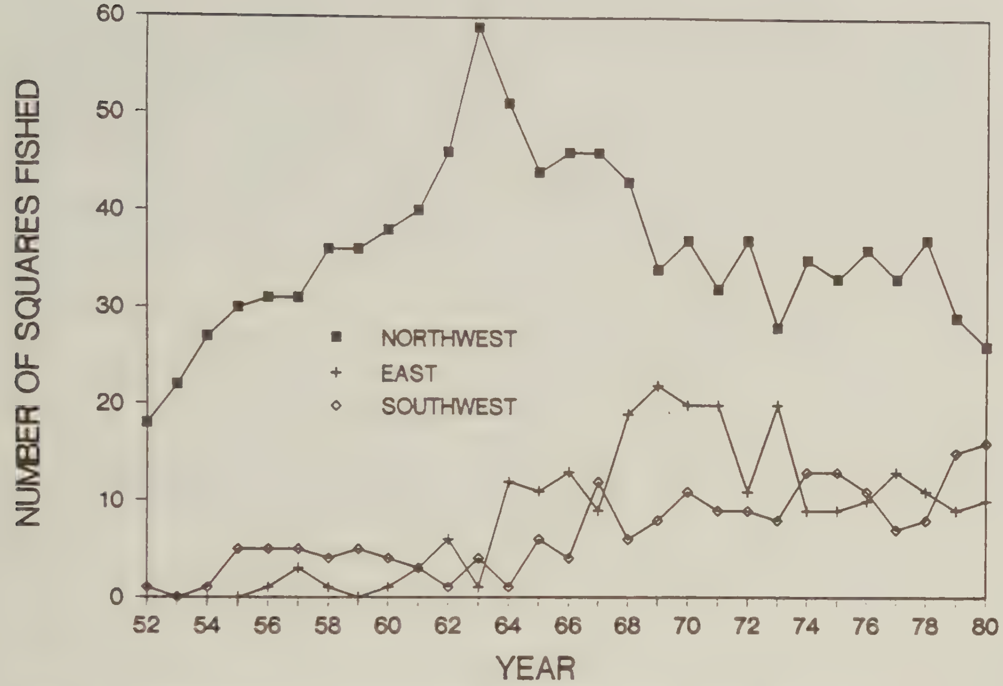


Figure 11. Annual distribution of 15% of the squares fished by the Japanese longline fishery in the Pacific Ocean producing the highest swordfish CPUEs in three hypothesized stock regions, northwest, southwest, and east.

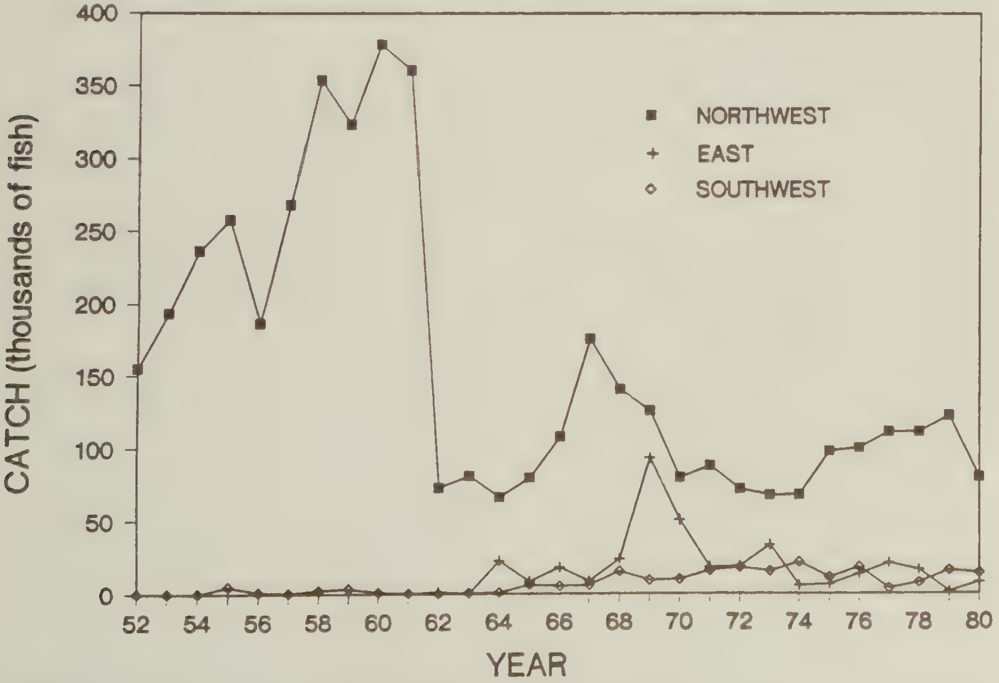


Figure 12. Annual distribution of swordfish catches from the Japanese longline fishery in the Pacific Ocean for squares fished that produced the highest swordfish CPUEs in three hypothesized stock regions, northwest, southwest, and east.

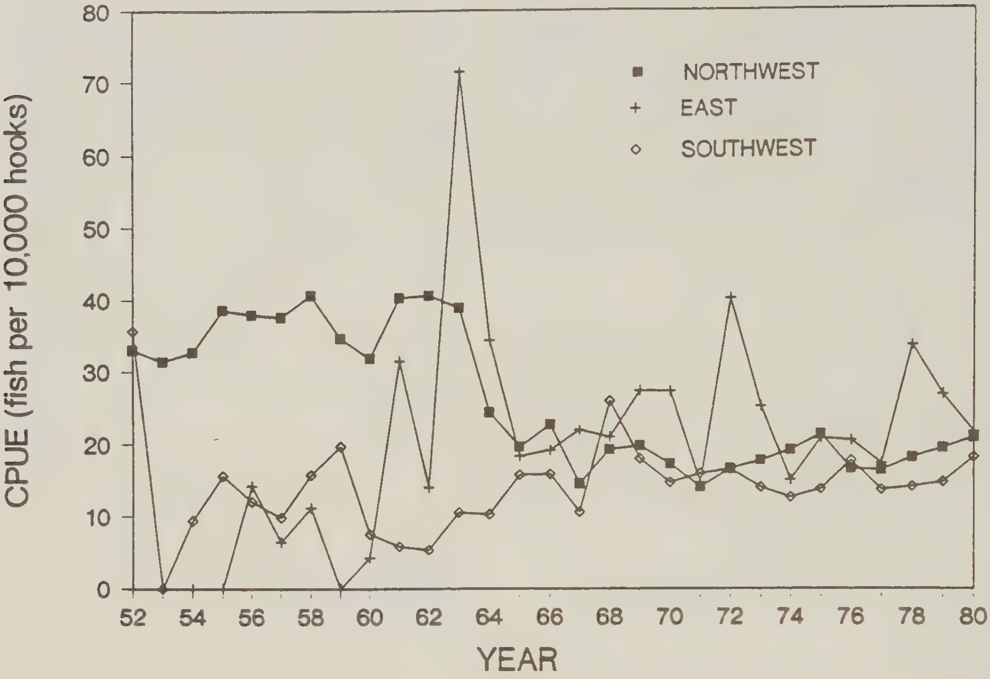


Figure 13. Annual distribution of catch-per-unit-effort by the Japanese longline fishery in the Pacific Ocean for squares fished that produced the highest swordfish CPUEs in three hypothesized stock regions, northwest, southwest, and east.

Fisheries Agency of Japan. 1965-1982. Annual reports of effort and catch statistics by area on Japanese tuna longline fishery, 1962-1980. Research and Development Department. Fisheries Agency of Japan.

Honma, Misao. 1973. Overall fishing intensity and catch by length class of yellowfin tuna in Japanese Atlantic longline.

MacCall, Alex D. 1983. Population models of habitat selection, with application to the northern anchovy. Ph.D. Dissertation. Univ. of Calif., San Diego. 170 p.

Sakagawa, Gary T. 1989. Trends in fisheries for swordfish in the Pacific Ocean. Current volume.

Sakagawa, Gary T., and Robert R. Bell. 1980. Swordfish *Xiphias gladius*. *In:* R.S. Shomura (ed.), Summary report of the Billfish Stock Assessment Workshop, Pacific Resources. U.S. Dep. Commerce., NOAA Tech. Memo., NOAA-TM-NMFS-SWFS-5.50-50 p.

Sakagawa, Gary T., Atilio L. Coan, and Norman W. Bartoo. In Press. Patterns in longline fishery data and bigeye tuna catches. Marine Fisheries Review (1988).

Shiohama, T. 1971. Studies on measuring changes in the characters of the fishing effort of the tuna longline fishery — I. Concentrations of the fishing effort to particular areas and species in the Japanese Atlantic fishery. Bull. Far Seas Fish. Res. Lab. Vol. (5):107-130. (Japanese with English summary).

Shomura, Richard S. 1980. Summary report of the Billfish Assessment Workshop, Pacific Resources: U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-5, 58 p.

Suzuki, Ziro, and Yukio Warashina. 1977. The comparison of catches made by regular and deep-fishing longline gear in the central and western equatorial Pacific Ocean. Unpublished MS in Japanese. Available as Translation No. 20, Southwest Fisheries Center, Honolulu Laboratory, Honolulu Hi.

Ueyanagi, Shoji. 1974. A review of the world commercial fisheries for billfishes. *In:* R.S. Shomura and F. Williams (eds.), Proceedings of the International Billfish Symposium. Kailua-Kona, Hawaii, August 1972, Part 2. Review and Contributed Papers. U.S. Dep. Commer., NOAA Tech. Rep., NMFS SSRF-657, p. 1-11.

Norman Bartoo earned a B.S. degree (fisheries management and administration), an M.S. degree (applied statistics), and a Ph.D. degree (population biology; 1977) at the University of Washington . From 1970-1977, he conducted research on the population dynamics and ecology of various fresh-water and anadromous fish populations in Alaska and Washington, designing and developing necessary sampling gear. Since 1977, he has investigated the population dynamics of tuna and billfish stocks worldwide, in the process evaluating and developing applicable population assessment models and methods. The results of his extensive research have been published in various scientific publications. His current position is that of leader of the tuna and billfish assessment and impact analysis program at the Southwest Fisheries Center of the National Marine Fisheries Service/NOAA at La Jolla, California.

Atilio L. Coan, Jr., earned the B.A. degree (applied mathematics) at San Diego State University. Since 1972, he has carried out research on tuna population dynamics, has developed data management systems and related computer software for fisheries for tuna and other large pelagics and for marine mammals; and has published accordingly in the scientific literature. Currently, he heads up the multispecies data collection and evaluation program of the NMFS/NOAA Southwest Fisheries Center at La Jolla.

8906

J. Mamm., 70(1):211-215, 1989

DIFFERENCES IN FEEDING HABITS BETWEEN PREGNANT AND LACTATING SPOTTED DOLPHINS (*STENELLA ATTENUATA*)

HANNAH J. BERNARD AND ALETA A. HOHN

National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038

Lactating mammals have higher energy requirements than all other mature adults and may need to eat greater quantities or change to a diet richer in nutrients (Brody, 1945, Close et al., 1985; Clutton-Brock et al., 1982, Perez and Mooney, 1986, Wright, 1984). When diets of cetaceans have been examined, however, the reproductive state of the animal rarely has been taken into account. In this study, we found a dietary difference between pregnant and lactating spotted dolphins (*Stenella attenuata*).

TABLE 1.—*Specimen number, date and time of day of collection, and minimum number of fish and squid consumed by pregnant and lactating spotted dolphins in the sample. Data for these specimens are freely accessible by the indicated specimen numbers through established data repositories at the United States National Oceanographic and Atmospheric Administration, Southwest Fisheries Center, La Jolla, California.*

Pregnant					Lactating				
Specimen	Date	Time	Squid	Fish	Specimen	Date	Time	Squid	Fish
DBH 765	14 Nov. 1975	0755	101	12	WAW 549	24 May 1978	0639	24	318
DBH 767	14 Nov. 1975	0755	213	5	WAW 532	20 May 1978	0734	43	297
WAW 524	27 Apr. 1978	0820	159	2	WAW 533	20 May 1978	0734	31	202
SLG 080	6 Dec. 1984	0842	8	87	STB 024	6 Apr. 1985	1043	66	40
JXB 001	2 Nov. 1979	0850	161	6	WAW 555	7 Oct. 1978	1132	97	106
LSL 025	25 Jun. 1980	0935	31	3	WAW 565	7 Oct. 1978	1132	23	16
PEL 316	14 Jul. 1985	1046	156	1	WSL 008	29 Jan. 1978	1205	1	33
WSL 018	29 Jan. 1978	1205	1	28	CER 001	26 Nov. 1979	1327	40	6
STB 005	1 Apr. 1985	1207	0	3	SOB 014	24 Nov. 1978	1435	92	1
SOB 013	24 Nov. 1978	1435	218	0	SRM 056	16 Feb. 1980	1438	9	855
SLG 091	6 Dec. 1984	1716	49	1	SRM 057	16 Feb. 1980	1438	25	585
					MBH 023	3 Oct. 1980	1702	1	22

We examined stomach contents of 11 pregnant and 12 lactating spotted dolphins collected by scientists and technicians of the U.S. National Marine Fisheries Service and Inter-American Tropical Tuna Commission on board purse-seiners of the yellowfin tuna (*Thunnus albacares*) fishery in the eastern tropical Pacific 15°N–10°S, 130°W–87°W from 1971 to 1985. Fishermen depend on these dolphins to locate tuna, and some dolphins are killed incidentally during the fishing operation. Dolphin stomachs were collected randomly on an opportunistic basis by the technicians. The specimens were distributed throughout the range of collection geographically, monthly, and by time-of-day (Table 1).

Initial data (e.g., specimen number, date of collection, and body length) on each dolphin were collected at sea. Dolphin pregnancy was determined by inspection of the uterus either in the field (for fetuses longer than 25 cm) or in the laboratory. Lactation was determined in the field by palpation and incision of mammary glands. Tissue samples also were collected at sea. Ovaries and uteri were preserved and stored temporarily in 10% formalin; stomachs were frozen at approximately −20°C.

Stomachs were thawed at the laboratory and the bolus was removed and sieved through screens of coarse to fine mesh (6.3 mm–180 μm). Only contents from the esophageal (or first) compartment were examined in this study because the most recently ingested meal is found largely in this chamber. Prey items were separated into categories of squid and fish. Undigested fragments of squid and fish tissue were weighed. Upper and lower squid beaks were counted, and the highest count of either was considered the minimum number of individual squid ingested. Similarly, left and right otoliths were separated and counted. The highest count of either was used as the minimum number of individual fish in the stomach.

The importance of prey type was evaluated by percent number, percent mass, and percent frequency of occurrence of prey (fish or squid) combined for all individuals within a stratum (pregnant or lactating) to calculate the index of relative importance (= % frequency of occurrence [% numerical frequency + % volume or mass] of a given prey item; Pinkas et al., 1971). Also, because of the skewed distribution of prey by mass in the stomachs of a given predator group (Amundsen and Klemetsen, 1986), and because our sample size (23 dolphins) is small, we calculated a sample variance of the proportion of squid in the stomachs, pooled for pregnant and for lactating dolphins, by bootstrap analysis (Efron, 1979, 1982). Differences in the observed proportion of squid between pregnant and lactating dolphins then was tested by application of the central-limit theorem using the following equation:

$$Z = \frac{\hat{P}_P - \hat{P}_L}{\sqrt{[\hat{V}(\hat{P}_P) + \hat{V}(\hat{P}_L)]}}$$

where

$\hat{P}_P$ = the observed proportion of squid from stomachs of all pregnant dolphins,
$\hat{P}_L$ = the observed proportion of squid from stomachs of all lactating dolphins, and
$\hat{V}$ = the variance estimated from 1,000 bootstrap replicates (with replacement), with each individual dolphin treated as a unit.

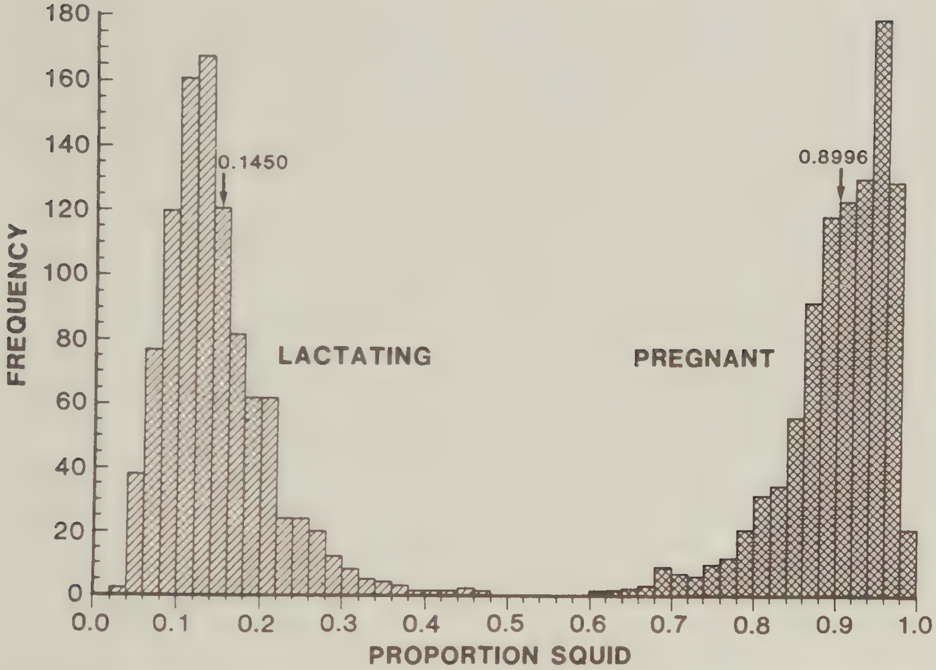


FIG. 1.—Frequency distributions for the mean proportion of squid in 11 pregnant and 12 lactating spotted dolphin stomachs calculated from 1,000 bootstrap replicate samples. The black box represents the one point of overlap between the mean proportions.

We used the nonparametric Mann-Whitney test to test for differences in stomach fullness (determined by dividing the mass of prey by stomach mass + prey mass; Fiedler and Bernard, 1987) between the two strata, and to test for differences in proportion of squid in stomachs of females collected before and after 1200 h (local time) within a stratum.

Fish and squid were the primary prey found in stomachs. The only crustaceans and mollusks found were a few isopods and pteropods, likely secondary prey. Most often only hard parts of prey remained, such as squid beaks and fish otoliths. The most frequently observed fish family was Exocoetidae, epipelagic flying fishes. There were some flotsam fishes (Nomeidae), followed by a few mesopelagic lantern fish (Myctophidae). The squid family most often represented was Ommastrephidae.

Both methods for evaluating prey importance showed that the diet of pregnant spotted dolphins differed greatly from that of lactating dolphins (Table 1). Pregnant dolphins consumed more squid by mass and proportion than did lactating dolphins. Conversely, lactating dolphins consumed more fish by mass and proportion than did pregnant dolphins. The index of relative importance for squid consumed by pregnant females was 7 times that of fish; the index for fish consumed by lactating females was approximately 8 times that for squid. Proportions of squid and of fish in the stomachs of pregnant and lactating dolphins were significantly different ($P < 0.0001$) using estimates of sample variance obtained from bootstrap techniques, resulting in rejection of the null hypothesis of no difference (Fig. 1).

There was some evidence ($0.05 < P < 0.10$) of a difference in stomach fullness between the two groups of females. The estimated difference is large (mean fullness of pregnant dolphin stomachs = 0.23, *SD* = 0.20; mean fullness of lactating dolphin stomachs = 0.47, *SD* = 0.40) considering our small sample size. This difference was not related to time-of-day effects. There was no significant difference in time of day on proportion of squid beaks found in the stomachs of females within a group (mean proportion of squid in pregnant females collected before noon = 0.83, *SD* = 0.33, and after noon = 0.50, *SD* = 0.56; mean proportion in lactating females before noon = 0.34, *SD* = 0.25, and after noon = 0.33, *SD* = 0.47).

Stomach-content data generally have been analyzed using contingency-table tests or the index of relative importance measure; the latter is an index of prey importance and not a statistical test. Crow (1982) recommended use of contingency-table analysis as a means of separating predator feeding modes. Commonly, prey items within a stomach are pooled, as if each prey item were an individual sample. Use of this approach is invalid because it requires the assumption that the prey items in the stomach of an individual are independent, that is, if an individual (dolphin in this case) takes a squid at one moment, the probability of taking a squid or fish at the next moment is totally unaffected. This probably is not the case for predators feeding predominantly on nocturnal, vertically migrating squid and epipelagic flying fish. The test is valid only if one prey item is selected at random from each predator. We have used the bootstrap method for obtaining a robust estimate of sample variance, enabling us to test statistically for differences in feeding habits between the two groups.

Perrin et al. (1973) examined stomach contents of 140 spotted dolphins collected in six net hauls of a tuna seiner from the same regions of the eastern Pacific as our samples. We were able to ascertain that the sex ratio from the first and second hauls was approximately 1:1 ($n = 57$) and only four females were lactating. The first haul was made before 1200 h, the second after 1200 h (in April 1968; W. F. Perrin, pers. comm.). Thus, their feeding habits may reflect those of the general population in this area. The dominant food item (in percent frequency, number, and occurrence) was squid for both hauls.

Barring major changes in feeding habits of spotted dolphins since 1968, our results indicate that feeding habits of pregnant females are similar to those of the population in general. Lactating females, which we found to consume mostly flying fish, seem to have altered their diet from the norm.

Lactating dolphins can satisfy the higher metabolic demand of producing milk either by increasing the quantity eaten or by selecting food of higher caloric value. In captivity, lactating bottlenose dolphins (*Tursiops truncatus*) consume more food than those not lactating, whereas pregnant dolphins do not appear to consume more food until just before parturition (S. H. Ridgway, pers. comm.).

The stomach-fullness test indicates that lactating spotted dolphins may have been eating more than pregnant ones. However, results of this test may be influenced by the interaction between time of day of sample collection and diurnal feeding habits, and by rate of digestion of prey. Lactating dolphins selected flying fish throughout the day and night, whereas pregnant dolphins consumed fewer flying fish than did lactating dolphins during day and night. Greater stomach fullness in lactating dolphins at least partially reflects their selection of a prey item available during the day, when samples are collected. Rate of digestion also influences the stomach-fullness results, but in the opposite direction. In both fish and mammals, a meal is digested faster when soon followed by another meal (Persson, 1984; Robbins, 1983). By eating flying fish, lactating dolphins may eat more frequently, thereby increasing their digestion rate over that of pregnant dolphins and possibly decreasing differences in stomach fullness.

The high, constant energetic cost of producing milk may necessitate that lactating females eat often. Although large whales are able to sustain a calf through several months without feeding (Lockyer, 1985), tropical dolphins have thin blubber (ca. 0.5 cm) thus, small energy reserves. In addition, their lactation period lasts 3–4 times longer than that of large whales (as long as 1.5 years; Myrick et al., 1986).

Lactating spotted dolphins may benefit from increased caloric or nutritional intake per gram of food by switching to fish. Fish and squid eaten by dolphins in the eastern tropical Pacific are different in caloric value (per 100 g muscle mass: $\bar{X} = 420$ kilojoules for fish and $\bar{X} = 290\text{–}330$ kilojoules for squid). Fish commonly eaten by dolphins in the North Pacific also have higher muscular lipid and energy values than squid from the same area (Sidwell et al., 1974). On the basis of the proximate composition of raw muscle in a flying fish (*Exocoetus volitans*) and an ommastrephid squid (*Ommastrephes bartrami*), flying fish is higher in protein and fat than squid, whereas squid is higher in water content (flying fish, $\bar{X}$ protein = 21.2% of wet mass, $\bar{X}$ fat = 0.9%, and $\bar{X}$ water content = 74.7%, from Sidwell, 1981; squid, $\bar{X}$ protein = 17.6% of wet mass, $\bar{X}$ fat = 0.34%, and $\bar{X}$ water content = 79.8%, from Croxall and Prince, 1982). Flying fish also have slightly more calcium and phosphorus, important for milk production (Sidwell, 1981).

Lactating females may consume more fish than squid to maintain water balance. The electrolytic balance is different between squid and fish. Squid are essentially isotonic with seawater, therefore, higher in $Na+$ and $Cl-$ than fish. By switching to a diet of flying fish, lactating dolphins help prevent additional water loss (Ridgway, 1972).

The behavioral restrictions imposed by a nursing calf may influence feeding habits of its mother. Most spotted dolphins in Perrin et al.'s (1973) study were feeding at greater depths than the tuna, thus avoiding direct competition. A female that dives deep to feed on squid may leave its calf vulnerable at the surface or reduce its own foraging success because the calf would not be able to dive for as long or as deeply. These restrictions would decrease the female's ability to catch squid at a time when its energetic requirements have increased. The alternative is for it to feed at or near the surface.

The behavioral restrictions and nutritional demands imposed by an altricial calf that nurses for >1.5 years are considerable. If the advantages of changing diet during lactation were primarily behavioral, we question whether maternal nutritional requirements could be satisfied because the main prey item for the rest of the population is squid. If the advantages were primarily nutritional, we question why the rest of the population also does not eat mostly flying fish when this food source can sustain a lactating female, unless it is to avoid competition with associated yellowfin tuna. Perhaps flying fish occur in less-dense schools, thus are less amenable to predation by large schools of predators. The actual reason that lactating spotted dolphins consume primarily flying fish may be a combination of several of these factors.

We thank K. A. Nagy, W. F. Perrin, A. J. Read, M. D. Scott, and E. F. Vetter for useful discussions about this study. S. T. Buckland and S C Chivers provided invaluable assistance in statistical analyses. We also thank R. L. Brownell, S. T. Buckland, D. P. DeMaster, R. J. Olson, W. F. Perrin, S. H. Ridgway, and M. D. Scott for providing critical comments on the manuscript.

LITERATURE CITED

AMUNDSEN, P-A., AND A. KLEMETSEN. 1986. Within-sample variabilities in stomach contents weight of fish—implications for field studies of consumption rate. Pp. 307–314, *in* Contemporary studies on fish feeding (C. A. Simenstad and G. M. Cailliet, eds.). Dr. W. Junk, Dordrecht, The Netherlands, 334 pp.

BRODY, S. 1945. Bioenergetics and growth. Reinhold Publ., New York, 1023 pp.

CLOSE, W. H., J. NOBLET, AND R. P. HEAVENS. 1985. Studies on energy metabolism of the pregnant sow. British J. Nutr., 53:267–279.

CLUTTON-BROCK, T. H., G. R. IASON, S. D. ALBON, AND F. E. GUINNESS. 1982. Effects of lactation on feeding behavior and habitat use in wild red deer hinds. J. Zool., 198:227–236.

CROW, M. E. 1982. Some statistical techniques for analyzing the stomach contents of fish. Pp. 8–15, *in* GUTSHOP '81, fish and food habit studies. Proc. third Pacific workshop (G. M. Cailliet and C. A. Simenstad, eds.). Washington Sea Grant Publ., Univ. Washington, Seattle, 312 pp.

CROXALL, J. P., AND P. A. PRINCE. 1982. Calorific content of squid (Mollusca: Cephalopoda). British Antarctic Surv. Bull., 55:27–31.

EFRON, B. 1979. Computers and the theory of statistics: thinking the unthinkable. Soc. Industrial Appl. Math., 21:460–480.

———. 1982. The jackknife, the bootstrap and other resampling plans. Soc. Industrial Appl. Math., Philadelphia, Pennsylvania, 92 pp.

FIEDLER, P. C., AND H. J. BERNARD. 1987. Tuna aggregation and feeding near fronts observed in satellite imagery. Continental Shelf Res., 7:871–881.

LOCKYER, C. 1985. Review of baleen whale (Mysticeti) reproduction and implications for management. Pp. 27–50, *in* Reproduction in whales, dolphins and porpoises (W. F. Perrin, R. L. Brownell, Jr., and D. P. DeMaster, eds.). Internat. Whaling Comm. Rept. (Special Issue 6), Cambridge, England, 495 pp.

MYRICK, A. C., JR., A. A. HOHN, J. BARLOW, AND P. A. SLOAN. 1986. Reproductive biology of female spotted dolphins, *Stenella attenuata*, from the eastern tropical Pacific. Fish. Bull., 84:247–259.

PEREZ, M. A., AND E. E. MOONEY. 1986. Increased food energy consumption of lactating northern fur seals, *Callorhinus ursinus*. Fish. Bull., 84:371–381.

PERRIN, W. F., R. R. WARNER, C. H. FISCUS, AND D. B. HOLTS. 1973. Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares*, in mixed-species aggregations. Fish. Bull., 71:1077–1092.

PERSSON, L. 1984. Food evacuation and models for multiple meals in fishes. Environ. Biol. Fishes, 10:305–309.

PINKAS, L., M. S. OLIPHANT, AND I. L. K. IVERSON. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. California Dept. Fish Game, Fish Bull., 152:1–84.

RIDGWAY, S. H. 1972. Homeostasis in the aquatic environment. Pp. 590–747, *in* Mammals of the sea (S. H. Ridgway, ed.). Charles C Thomas, Publisher, Springfield, Illinois, 812 pp.

ROBBINS, C. T. 1983. Wildlife feeding and nutrition. Academic Press, New York, 343 pp.

SIDWELL, V. D. 1981. Chemical and nutritional composition of finfishes, whales, crustaceans, mollusks and their products. Natl. Oceanographic Atmos. Admin., Tech. Memo. Natl. Marine Fish. Serv., F SEC-11,432 pp.

SIDWELL, V. D., P. R. FONCANNON, N. S. MOORE, AND J. C. BONNET. 1974. Composition of the edible portion of raw (fresh or frozen) crustaceans, finfish, and mollusks. I. Protein, fat, moisture, ash, carbohydrate, energy value, and cholesterol. Marine Fish. Rev., 36:21–35.

WRIGHT, P. C. 1984. Biparental care in *Aotus trivirgatus* and *Callicebus moloch*. Pp. 59–75, *in* Female primates: studies by women primatologists (Meredith F. Small, ed.). Alan R. Liss, New York, 272 pp.

Submitted 4 June 1987. Accepted 23 February 1988.

Drift Net Problems Spread to South Pacific

by George W. Boehlert

■ Like video games and hamburgers, drift gill net fishing (drift netting) is becoming commonplace throughout the world. Its latest emergence is in the relatively unfished waters of the South Pacific by Taiwanese and Japanese drift net fleets targeting surface schools of albacore. Concerned fishery officials of several South Pacific island countries met in Suva, Fiji, on November 3 and 4, 1988, to discuss ways to discourage the use of drift nets on the high seas of the South Pacific, according to Dr. George W Boehlert, Director of the Honolulu Laboratory, NOAA Fisheries—Southwest Region.

"This highly effective fishing technology brings with it considerable controversy and a host of knotty problems for fishermen, marine scientists and government fishery managers," said Dr. Jerry A. Wetherall, an albacore expert and chief of the Honolulu Laboratory's Pelagic Resources Investigation, who attended the meeting. "One of the main problems is that drift nets entangle and kill other marine life occurring in the same area as the target fish species."

"Drift net fishing occurs legally on the high seas, so the South Pacific fishery officials considered means to discourage drift netting in the region by reducing economic incentives," said Wetherall. Albacore are the premium species of tuna for canning and a resource of considerable interest to South Pacific islanders.

Albacore gill netting on the high seas is economically attractive to its proponents because nets 15 miles or more in length, reaching from the sea surface down to 30 feet, can be set in the water, left to drift in the current overnight and hauled in at relatively low cost. The nets are made from multifilament nylon and have meshes about 7 to 8 inches wide.

Large albacore have been harvested for 30 years in deep waters of the South Pacific by fleets of longline fishing vessels from Japan, Taiwan and Korea operating out of ports in Asia or the South Pacific. Recently it was discovered that smaller albacore could be caught in a narrow zone of the South Pacific stretching from New Zealand to Chile near 40 degrees south latitude. In that area, water of the temperature preferred by albacore occurs at the sea surface, coincident with a zone relatively rich in forage. Albacore aggregate there to feed and are vulnerable to surface trolling and drift netting as well as longlining.

Two trollers from the United States began a fishery in the area in 1986, followed by seven trollers in 1987. In the 1988 fishing season, a fleet of 41 U.S vessels was joined by trollers from Canada, Fiji and French Polynesia. The troll fishery was so successful that several South Pacific island countries consider it a promising avenue for local economic development.

In 1988 drift net fishing began on a small scale in the same area fished by the trollers. However, during the upcoming 1989 fishing season, January through April, the fleet of drift net boats is expected to grow to as many as 80 vessels, each with a capacity of 200 to 300 tons of albacore. Some concern exists that the increased catch of albacore by drift net vessels, when combined with the catch already taken by longline and trolling fleets, may exceed the maximum sustainable yield of the population.

This situation is complicated by the fact that the actual mortality caused by drift net fishing may be substantially greater than the observed catch. Some of the fish and other marine life entangled in the nets drop out during fishing and retrieval of the nets, and an unknown fraction of albacore dropping out die as a result of the encounter. Others suffer cuts and abrasions that reduce their value to troll and longline fishermen who may catch them later.

Troll fishermen also report that albacore behavior is affected by encounters with drift nets, reducing the effectiveness of troll fishing.

The incidental mortality associated with albacore drift netting in the South Pacific is a potential problem. The incidental catch may include marlin, swordfish, seabirds, sea turtles and marine mammals. Such species as the southern fur seal and beaked whale may be at risk. Other methods of catching albacore, such as trolling or longlining are not detrimental to seabirds, sea turtles or marine mammals.

Another major problem caused by drift nets is the hazard they impose to fishing vessels and fishermen at sea. The nets are operated at night and are set at the water's surface, where they can easily entangle the propellers of vessels. Trolling vessels, and even the drift net vessels themselves, have become disabled by drift nets. Fishermen are endangered when they are forced to dive under the vessel to cut the boat free. During gill netting trials a few years ago in waters north of Australia, two Japanese fishermen drowned in such an effort.

The Suva meeting, which was called by the South Pacific Forum Fisheries Agency, was attended by representatives from American Samoa, the Cook Islands, New Zealand, Fiji, French Polynesia, Tonga and Vanuatu, as well as officials from the South Pacific Commission, the United Nations Development Program and South Pacific island fishing companies. Wetherall provided the group with technical information about the albacore resource and fisheries.

According to Wetherall, one of the means considered by the South Pacific fishery officials to discourage albacore drift netting was for countries in the region to deny drift net vessels access to their exclusive economic zones or ports for any purpose, such as reprovisioning, refueling or transfer or delivery of catches.

"Another measure considered was for officials to persuade the canneries and transshipment facilities in the South Pacific to deal only in albacore caught by trollers and longliners, and not drift netters," said Wetherall.

The use of drift gill nets by foreign vessels has been banned within the 200-mile exclusive economic zone around Hawai'i, Guam and American Samoa. The actions taken by the South Pacific island countries add to the growing global resistance to drift net fishing and show that concerns about negative effects of drift netting exist even in the remote waters of the South Pacific.

. . . **George**

8908

Distribution of larval fishes around an isolated oceanic island and the role of larval retention in population maintenance (Abstract)

George W. Boehlert, William Watson, and L. Charles Sun

Ichthyoplankton sampling was conducted in November 1984 in waters surrounding Johnston Island (16°44′N 169°32′E), a small, isolated atoll in the central Pacific Ocean. The typical flow pattern in this region is westward; the nearest island is in the Hawaiian Chain, 760 km distant. Discrete-depth sampling with a $1\ \mathrm{m}^2$ Tucker trawl was concentrated in the upper 100 m, where larval abundances were greatest. Concurrently, a grid of CTD and XBT stations was occupied to later estimate patterns of geostrophic currents. Most collections were dominated by oceanic taxa. In the 0–50 m stratum, larval densities were relatively uniform, but densities at greater distances tended to be slightly lower. In the 50–100 m stratum, however, abundances on the west (downcurrent) side of the island were markedly higher than either upcurrent or further downcurrent. Oceanic taxa (as exemplified by the Myctophidae) did not display this pattern, while marked areas of very high abundance characterized the island-related taxa. The species responsible for most of the increased abundance was the gobiid *Eviota epiphanes*. Geostrophic flow patterns indicated that this region was one of return flow associated with mesoscale eddies north and west of the island. This region may serve as a downcurrent retention area for the pelagic larvae of island-related taxa, and may facilitate recruitment back to the source populations. Population maintenance of species with pelagic larvae in tropical islands is poorly understood, but processes in the plankton are probably responsible for recruitment variability. More detailed measurements of currents and finer scale resolution of the vertical distribution of larvae will be necessary to understand these mechanisms of larval retention. Variability in the physical patterns may then be investigated to determine the effects on recruitment variability.

George W. Boehlert: NMFS, Southwest Fisheries Center Honolulu Laboratory, 2570 Dole St., Honolulu, HI 96822-2386, USA. William Watson: Marine Ecological Consultants, Encinitas, CA 92024, USA. L. Charles Sun: Department of Oceanography, University of Hawaii, Honolulu, HI 96822, USA.

8909

Time Series of Growth in the Genus *Sebastes* from the Northeast Pacific Ocean

George W. Boehlert, Mary M. Yoklavich, and Dudley B. Chelton

ABSTRACT: Marine fish populations respond to their physical and biotic environment in complex ways. While direct studies may discern short-term responses at the individual level, time series are needed to describe or predict the population level response to environmental variation or cycles. The ageing technique presented in this paper extracts historical growth information from otoliths through sectioning and careful measurement in order to establish time series of growth. Otoliths of two long-lived species, *Sebastes pinniger* and *S. diploproa*, were collected off the west coast of North America in 1977–84. Fish ages ranged from 1 to 86 years; corresponding birth dates were as early as 1896. Otolith measurements allow description of growth at ages 1–6 for several decades of this century. Although the technique has certain limitations, significant interannual variability in growth is observed, and its relationship to the species' environment is interpreted. Within species, coherence in growth among age groups was not always evident; first year growth in *S. diploproa* was particularly different from growth in other years. For both species, growth responses to environmental factors were not clear; the dominant signal in the time series appears to be increased growth rates after about 1970. This signal is apparently related to density-dependent factors (most likely prey availability) associated with stocks depleted by fishing pressure.

Long-term changes in marine fish populations can be caused by physical and biotic factors as well as man-induced changes. An important goal of fisheries research is to evaluate the effect of fishing on population levels, and this task is easily accomplished if natural variability is understood. Determining causal relationships and superimposing fishing mortality can lead to predictive capability; indeed, many studies in fisheries oceanography model past changes in fish stocks with the objective of forecasting future trends in populations for purposes of fisheries management. Long-term biological data sets are also valuable for ecosystem research, particularly in evaluating the range of natural variability (Wolfe et al. 1987). Historical catch records have been used to assess long-term changes in marine fish populations or stock sizes, and such data from many decades are available for some Pacific salmonid stocks (Mysak et al. 1982; Rogers 1984), for several North Atlantic fisheries (Cushing 1982), and in the Southern Hemisphere for Tasmanian fish populations (Harris et al. 1988). Changes in species assemblages and biotic interactions in the California Current region have been described on both the decade scale (Loeb et al. 1983; Moser et al. 1987) and the century scale (Soutar and Isaacs 1974).

Long-term time series are developed either from continuous data collection or by the extraction of information stored naturally as a chronographic record. Continuous data collection must occur over generations of biologists; starting a new series may not allow achievement of objectives for 30 or more years, so available time series, which are often collected for other purposes, are used. A classic example of extracting data from a chronographic record is the study of fluctuations in population abundance of *Engraulis mordax*, *Sardinops sagax*, and *Merluccius productus* by Soutar and Isaacs (1974). By enumerating fish scales preserved at different depths in anoxic, varved sediments, they defined natural cycles of abundance of these species over 150 years. This approach has recently been applied by Shackleton (1987). Chronological information is also stored in fish otoliths (Radtke 1984; Campana and Neilson 1985). Estimating age of fishes and using otoliths for back calculation are simple examples of extraction of historical information. In addition, the isotopic composition of otoliths has been used to define past thermal habitats occupied by individual fish (Mulcahy et al. 1979; Radtke 1987) and to identify stocks (Mulligan et al. 1987).

George W. Boehlert, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96822-2396, and Joint Institute of Marine and Atmospheric Research, University of Hawaii, Honolulu, HI 96822.

Mary M. Yoklavich, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98115-0070.

Dudley B. Chelton, College of Oceanography, Oregon State University, Corvallis, OR 97331-5503.

Manuscript accepted June 1989.
Fishery Bulletin, U.S. 87: 791–806.

Because studies on fish growth are generally conducted at a single time, time series on the order of several decades are either rare or absent. Some available time series are often produced from different studies, which may not have used the same techniques for sampling, ageing, or interpretation (Boehlert and Kappenman 1980). Using fish scales and interopercular bones from two flatfish species collected over approximately 15 years, Kreuz et al. (1982) established time series of growth and found that growth was negatively correlated with temperature. Width and length of otoliths can be used to estimate length of fish so that past growth patterns can be estimated with back-calculation techniques on otoliths from older fish. Extreme longevity has been documented in the scorpaenid genus *Sebastes* (Bennett et al. 1982; Leaman and Nagtegaal 1987), and ages in excess of 80 years have been reported for several species (Archibald et al. 1981; Boehlert and Yoklavich 1984; Leaman and Beamish 1984). Thus, otoliths of these species can potentially be used to estimate growth from several decades ago.

In this paper, we describe an otolith-based technique for obtaining a historical time series of growth. We apply this technique to two species, the canary rockfish, *Sebastes pinniger*, and the splitnose rockfish, *S. diploproa*, and describe the resultant time series of growth in light of physical and biological factors.

MATERIALS AND METHODS

Otoliths from *S. pinniger* and *S. diploproa* were collected during rockfish surveys conducted by the Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, in 1977 (Boehlert 1980), 1980 (Boehlert and Yoklavich 1984), and 1983 (Wilson 1985). Collection techniques followed Gunderson and Sample (1980). Our objective was to represent as many years of growth as possible; therefore, otolith selection was based upon age alone, and old fish greatly outweighed their relative abundance in a random sample. Additional otoliths from *S. pinniger*, collected off the central Oregon coast in 1984, were obtained from the Oregon Department of Fisheries and Wildlife.

Technical aspects of our methods, described in Boehlert and Yoklavich (1987), are repeated here for completeness because the original information is not widely available. For otolith sectioning and age determination, we followed Boehlert and Yoklavich (1984). Briefly, otoliths were affixed to cardboard tags, embedded in polyester casting resin, mounted on a diamond lapidary saw, and fed onto a pair of thin diamond blades separated by acetate spacers. Dorsal-ventral sections through the focus and perpendicular to the sulcus, approximately 0.4 mm thick, were removed from the center of the otolith, attached to microscope slides, and ground to eliminate artifacts. Total ages were determined from these sections by identifying the first translucent annulus (winter growth zone) and counting sequential growth zones from the center toward the dorsal edge; dorsal annuli at ages near 8–10 years were followed from the dorsal edge to the interior dorsal quadrant, and subsequent annuli were counted to the internal surface.

Annulus measurements, used as a proxy of annual fish growth, were limited to the first 6 years of growth. This limit was imposed because otolith increments became smaller with increasing age; eventually, linear growth stopped, and the otolith began to thicken (Bennett et al. 1982; Boehlert 1985). Two different techniques for otolith measurement were used. In the faster growing *S. pinniger*, whose otoliths are clearer, measurements were from the focus to the dorsal distal edge of each increment (Fig. 1). In *S. diploproa*, whose otoliths are typically more opaque and whose annual increments are smaller, the focus was difficult to identify; for this species, measurements were from the dorsal to ventral distal edges of increments 1–6.

Data from each fish included sex, fork length, date of collection, location, total age, and widths of the increments measured from the otoliths for ages 1–6. The first increment width was a true reflection of first year growth; subsequent measurements, however, integrated past growth. That is, a large growth increment in year 1 could bias the measurement in years 2–6. To remove this correlation and to provide a measure of growth in each year, our analysis used growth increments (GI(i), where i = 1–6) determined by differencing successive measurements. Thus, growth in a given year was not cumulative and generally did not reflect past growth.

Age was subtracted from the year of collection to determine the year of birth. For each fish, each growth increment (1–6) was associated with a specific "year of growth" in the following manner: Increment 1 represented the year of birth or first year growth; increment 2 represented the following year, and so forth. Data on 6 years of growth were available for each fish with the ex-

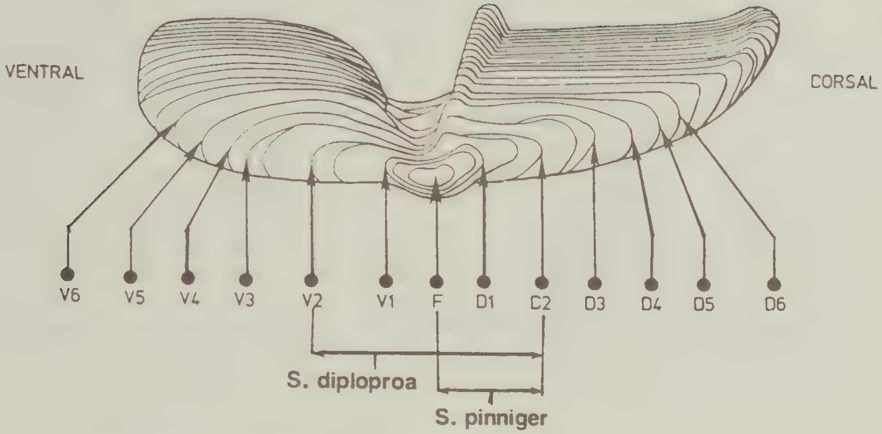


FIGURE 1.—Schematic drawing of an otolith section from *Sebastes* spp. showing the axes of measurements. Measurements for *S. pinniger* were from focus to dorsal distal increment margin (i.e., F to D2); measurements for *S. diploproa* were from dorsal to ventral distal increment margins (i.e., V2 to D2).

ception of those younger than 6 at the time of sampling. As an example, a fish collected in 1980 and aged at 40 years was determined to be born in 1940; therefore, growth measurements from this individual were available for years 1940 (GI(1)) through 1945 (GI(6)).

Most otoliths in our study were from males; otoliths from older females were also included to increase the sample size earlier in the time series. Length at age for these species did not differ between sexes until after sexual maturity, which occurred after age 6 (Boehlert 1980; Boehlert and Kappenman 1980). Still, to test for differences in growth between sexes, we separated the data by sex and then aggregated the data for each GI(i) so that each year of birth had a single, mean value. A paired t-test was used to test for differences in respective growth increments for all years in which both male and female data were available. Growth did not significantly differ between sexes for either species ($P > 0.10$), so data were combined in subsequent analyses.

Certain aspects of the technique, associated with errors in otolith increment measurement and age estimation, may have led to variability in results. From a methodological standpoint, three errors were quickly apparent. First, small changes in the location where the section was removed from the otolith (Fig. 1) may have resulted in slightly different increment measurements; we expected this to introduce relatively minor errors, however, since the sectioning technique (Boehlert and Yoklavich 1984) was designed to be the same. The second source of error occurred in the estimate of total age. Errors in this estimate will result in the assignment of an incorrect year of birth and, thereby, incorrect years of growth for each growth increment; this type of error is probably the most serious, because it will tend to decrease the reliability of real differences between adjacent years. This type of error will increase with increasing age (Boehlert and Yoklavich 1984), and therefore, the reliability of between-year differences in growth will decrease somewhat with increasing age. Finally, errors in selection of annuli (for example, selecting 2–7 instead of 1–6) can occur when making measurements on the section. The cumulative effects of these errors, averaged over many individual samples for each year, should not significantly mask long-term trends in the data. The errors could mask correlations with high frequency environmental features but should not affect correlations with low frequency phenomena.

An additional concern stemmed from the implicit assumption that there is no linkage between longevity and growth; this concept, associated with Lee's phenomenon, is related to size-selective mortality (Ricker 1969). If long-lived individuals are characterized by either faster or slower growth rates during the first 6 years of life than are individuals with shorter lifespans, then we can encounter problems comparing growth of young and old fishes. In lightly exploited populations of *S. alutus*, for example, very old age groups may have smaller mean lengths than younger age groups, suggesting some type of growth-dependent mortality (Leaman[1]). Markedly smaller mean lengths at age have not been observed, however, for very old specimens of either *S. pinniger* or *S. diploproa* (Boehlert and Yoklavich 1984; Wilson 1985). A genetic basis for differences in growth and age at sexual maturity has been suggested for cod, *Gadus morhua* (Borisov 1979) and brown trout, *Salmo trutta* (Favro et al. 1979). An investigation of the biochemical genetics of *S. diploproa* by using electrophoresis at 29 loci has shown no variation associated with age (L. W. Seeb and G. W. Boehlert unpubl. data). Although negative results cannot rule out a difference, our growth results did not show a consistent trend supporting a genetic basis for growth differences.

Data Analysis and Interpretation

Yearly means of GI(i)'s were calculated and were the values upon which further analysis was made. Standardized growth anomalies (Z-scores) were calculated so that each time series of growth for both species had a mean of zero and a standard deviation of one. This allowed comparison of the growth anomalies in different growth years, standardized for the effects of growth increment magnitude. Comparisons between species were also facilitated by this conversion. A growth anomaly value of zero corresponded to normal growth rate, averaged over the period of the data record.

Within species, there were both similarities and differences between the time series of different age groups. Covariability between different age groups was extracted by principal component analysis (Hotelling 1933) of the six-by-six cross correlation matrix, which expressed interrelationships among the six series of standardized growth anomalies of each species over the period of analysis. The principal component expansion of growth increments can be written as

$$\mathrm{GI}(x,t) = \sum_{n=1}^{6} F_n(x) a_n(t); \qquad (1)$$

where x is the age class (1–6), t is time, and the index n corresponds to component number (1–6). The loadings $F_n(x)$ are the eigenvectors of the cross correlation matrix. The amplitude time series $a_n(t)$ are referred to as the principal components of covariability. The dominant loadings across age groups (those reducing the largest proportions of total variance in the original data set) and the associated principal component time series were interpreted in terms of physical and biological processes influencing growth rate variability. An attempt was made to relate the principal component time series as dimensionless, uncorrelated expressions of growth for each species to time series of environmental and biological data. Environmental data (upwelling, wind speed, and wind stress curl at lat. 45°N, long. 125°W; sea-surface temperature at Neah Bay, WA, lat. 48°22′N) from 1946 to 1977 were provided by the Pacific Fisheries Environmental Group, Monterey, CA. Sea level data from San Francisco (lat. 38°N) were taken from Prager and MacCall[2].

RESULTS

A total of 942 *S. pinniger* (616 males and 326 females) and 802 *S. diploproa* (651 males and 151 females) were used in this study. Specimens of *S. pinniger* ages 2–60 years corresponded with birth dates from 1920 to 1978 (Fig. 2A); *S. diploproa* ages 1–86 years corresponded with birth dates from 1896 to 1979 (Fig. 2B). Total numbers of growth increments measured were 5,600 for *S. pinniger* and 4,714 for *S. diploproa*.

Mean annual size of growth increments for both species showed a reduction with age group, which is typical in fishes. Mean size of increments decreased dramatically (between twofold and threefold) from age groups 1 and 2, then slowly from age groups 2–6 (less than twofold). Growth anomalies for all ages were characterized by significant interannual variability for both species (Figs. 3, 4). The standardized time series for *S. pinniger* (Fig. 3) showed a general, gradual decreasing trend in growth rates for age groups 2–4 from the beginning of the record until about 1965 or 1970. Age group 1 showed a generally decreasing trend prior to about 1957 and an increasing trend thereafter. Age groups 5 and 6 showed a gradually increasing trend virtually

---

[1] B. M. Leaman, Pacific Biological Station, Nanaimo, B.C., Canada, pers. commun. November 1987.

[2] Prager, M. H., and A. D. MacCall. 1986. An environmental data base describing coastal southern California in the years 1920–1984. Part 1: Procedures and summaries. Natl. Mar. Fish. Serv., Southwest Fish. Cent. Adm. Rep. LJ-86-31, 50 p.

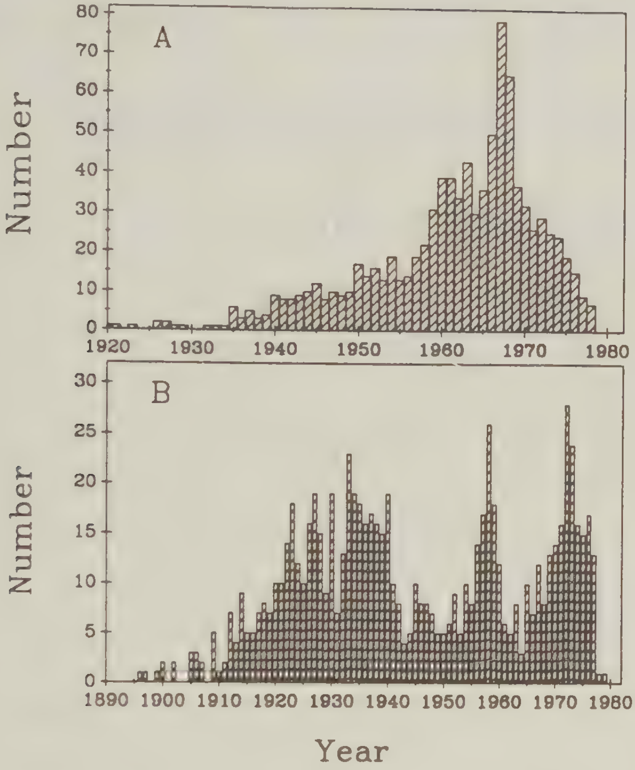


FIGURE 2.—Distribution of the years of birth; males and females are combined. A. *Sebastes pinniger*. B. *S. diploproa*.

throughout the time series. After about 1972, all age groups showed concordance in a relatively abrupt increase in growth rates. This increase may have been shorter lived for age groups 5 and 6, as suggested by the decrease in positive growth rates for the last few years of the record. Positive growth rates continued to increase to the end of the record in the 5 yr running averages for age groups 1–4, though with some significant year-to-year variability in the yearly data.

The time series for *S. diploproa* (Fig. 4) was much longer than for *S. pinniger* (Fig. 3). Age groups 2–4 generally showed a gradual decreasing trend in growth rates prior to about 1965 or 1970. This pattern was similar to that observed for *S. pinniger* age groups 2–4 over the more limited record length. This long-term trend in decreasing growth rates was less evident in *S. diploproa* age groups 1, 5, and 6. Growth rates for age group 5 were nearly normal throughout the record. Growth rates for age group 6 were relatively low in the early part of the record and slightly higher than normal for the period 1930–55. They decreased briefly from 1955 to 1960, then were steady, near-average, or slightly increasing until about 1970. Age groups 2–6 of *S. diploproa* increased in growth rates during the 1970's, coinciding with the high growth rates of all age groups of *S. pinniger* after about 1972. Growth rates for age group 1 of *S. diploproa* were strikingly different from all other age groups of both species of *Sebastes*, with a predominance of variability over much shorter time scales (ca. 5 years) and no evidence of a rapid increase during the 1970's.

The relationship between growth variability in different age groups summarized above from the time series in Figures 3 and 4 were compactly described by the principal components of the six age group time series. We included only years for which yearly mean values of growth were

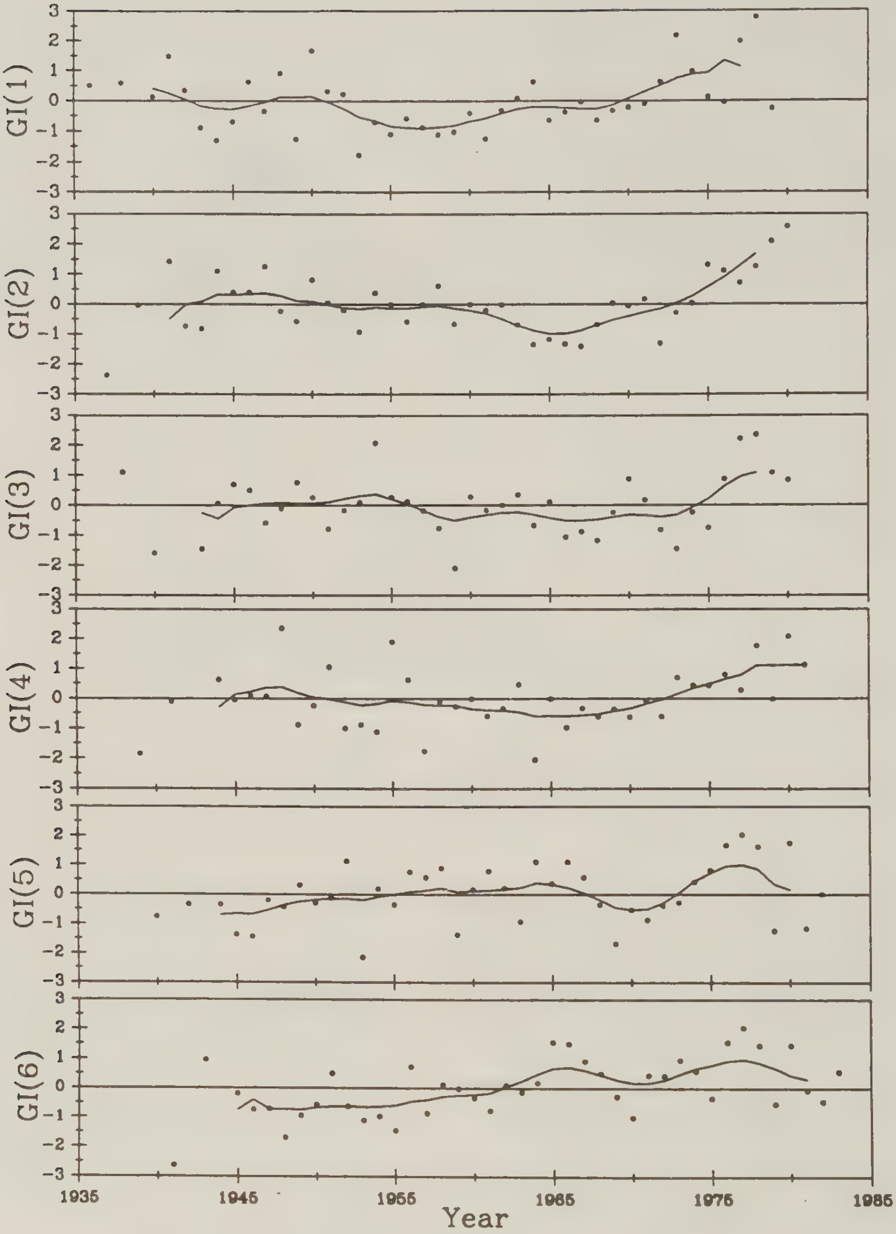


FIGURE 3.—Plot of mean growth anomalies in years of growth 1–6 for *Sebastes pinniger*. Data points represent the yearly mean growth anomalies; the curve represents the double 5-yr running average. Only years with means based upon four or more observations are used.

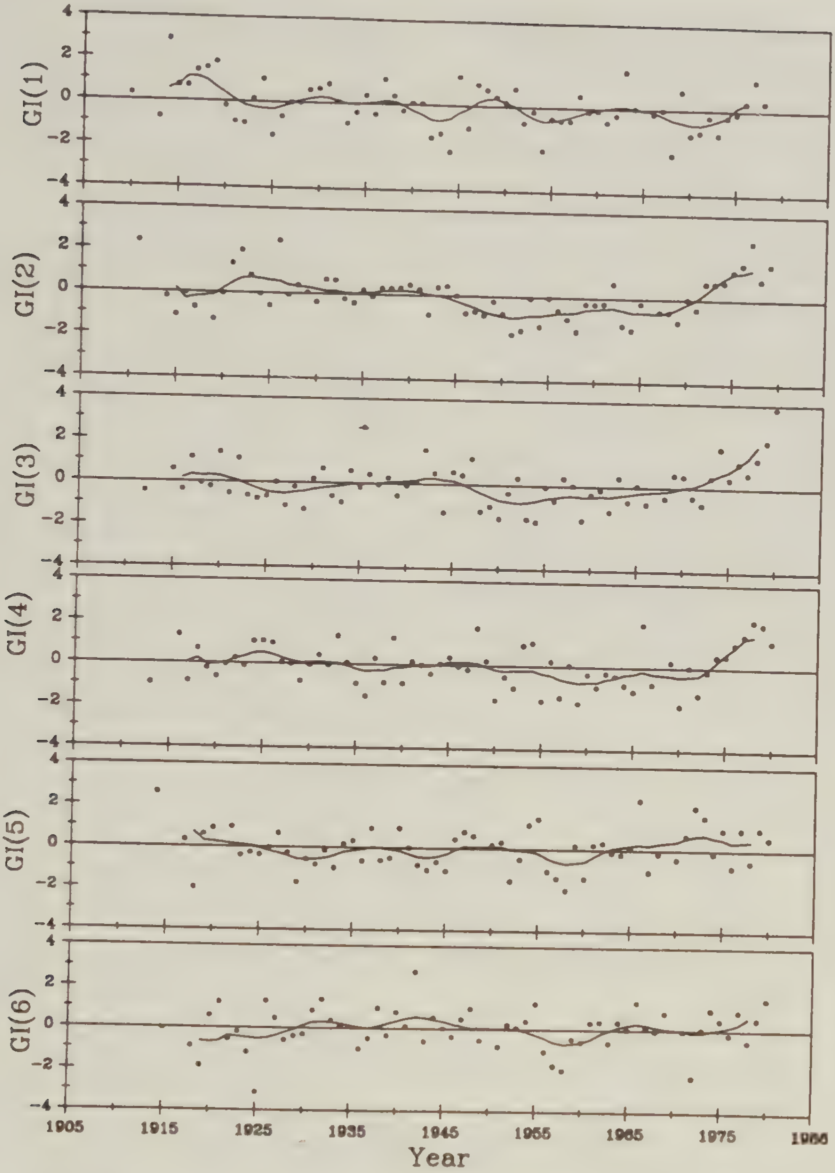


FIGURE 4.—Plot of mean growth anomalies in years of growth 1–6 for *Sebastes diploproa*. Data points represent the yearly mean growth anomalies; the curve represents the double 5-yr running average. Only years with means based upon four or more observations are used.

computed from four or more observations. The first three principal components of *S. pinniger* variability explained 75% of the total variance summed over the six growth anomaly time series; loadings are shown in Figure 5A. Corresponding principal component time series (Fig. 6), or "modes of variability," effectively filter the data to draw attention to the dominant signals discussed above (Fig. 3). By considering the loading values (and thus the relative contribution of each age class) along with the trends in the principal component time series, we described the dominant signals in the time series of the original data. The loadings of the first mode were approximately the same for all six age groups (Fig. 5A); this principal component represented the dominant mode of coherent variability with about the same amplitude in all age groups. The corresponding principal component time series (Fig. 6) is nearly averaged from 1940 to 1970, followed by an abrupt increase beginning about 1972, and represented the high growth rates for all age groups after 1972 (cf. Fig. 3). This was the most pronounced signal in the record, accounting for 36% of the variability over the six age groups.

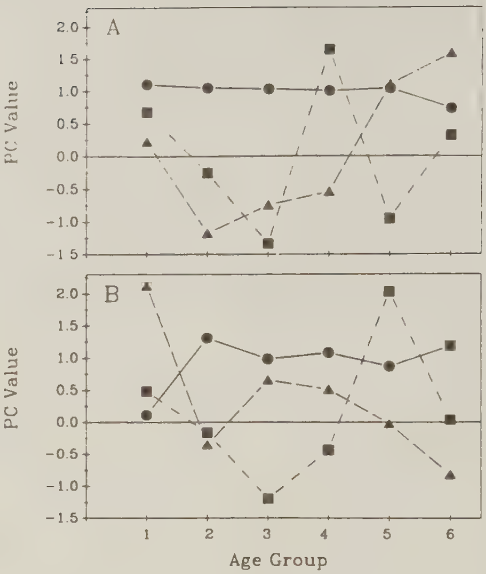


FIGURE 5.—Component (age group) loadings to the three principal components (PC's) explaining the greatest amount of variability in the growth time series. A. *Sebastes pinniger*. B. *S. diploproa*. Circles represent the loadings of the first PC, triangles the second, and squares the third.

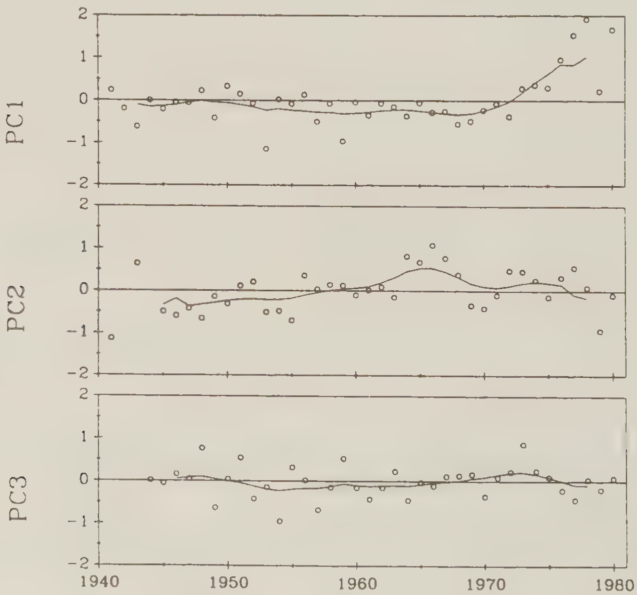


FIGURE 6.—Principal component time series for the three modes explaining 75.0% of the total variance in growth of *Sebastes pinniger* from the six time series in Figure 3. The curve represents the double 5-yr running average.

The second principal component of *S. pinniger* growth variability extracted the coherent trends in the time series evident prior to 1965 (Fig. 3). The loadings (Fig. 5A) were negative for age groups 2–4 and positive for age groups 5 and 6; the loading value for age group 1 was zero, indicating that its variability is not related to this mode. The principal component time series of this second mode of variability (Fig. 6) generally showed a gradually increasing trend from 1945 to 1965, followed by a decreasing trend thereafter. This time variability described well the trends evident in Figure 3 for age groups 5 and 6, for which the loading values (Fig. 5A) were positive. Since the loading values of the second mode were negative for age groups 2–4 (Fig. 5A), this mode of variability (the product of the loading value and the principal component time series, see Equation (1)) corresponded to a gradually decreasing trend in age groups 2–4 growth rates prior to 1965, followed by an increasing trend thereafter. We have no explanation for the difference in the early trends in growth between age groups 5 and 6 and age groups 2–4. Further, growth increments in 1964–68 (Fig. 3) reinforced this difference and produced a peak in the principal component time series in those years (Fig. 6). This second mode of variability describing the trends in growth rates accounts for 24% of the variance in the data.

The loading values of the third principal component of *S. pinniger* growth variability (Fig. 5A) showed no obvious coherent relationship among age groups. The values oscillated from positive to negative among the age groups, and the corresponding principal component time series (Fig. 6) showed no remarkable characteristics. Thus, this mode of variability has no obvious physical interpretation.

The first four principal components of *S. diploproa* variability explained 81% of the total variance summed over the six growth anomaly time series; the loadings for the first three modes are shown (Fig. 5B), with corresponding principal component time series (Fig. 7). The loading values of the first principal component, accounting for 30% of the variance, were approximately the same for age groups 2–6 and zero for age group 1. This highlighted the fundamental difference between growth rate variability in age group 1 and that in the other age groups.

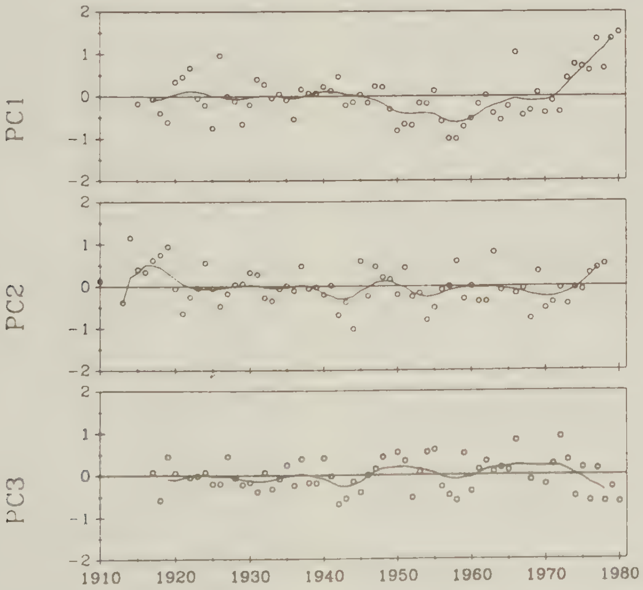


FIGURE 7.—Principal component time series for the three modes explaining 64.6% of the total variance in growth of *Sebastes diploproa* from the six time series in Figure 4. The curve represents the double 5-yr running average.

The principal component time series of this first mode of variability (Fig. 7) showed growth rates as nearly normal in 1915–45, moderately decreasing in 1945–70, and abruptly increasing after about 1972. This was consistent with the earlier interpretation of variability in the individual time series (Fig. 4). The increased growth rates after 1972 coincided with the same signal described by the first principal component of *S. pinniger* growth rates (Fig. 6).

The second principal component of *S. diploproa* growth rates extracted the independent nature of variability in age group 1 and accounted for 19% of the total variance over the six growth anomaly time series. The loading values of this second mode of variability (Fig. 5B) were near zero for all age groups except age group 1. The corresponding principal component time series (Fig. 7) was almost identical to the time series of *S. diploproa* age group 1 (Fig. 4); periods of positive, normal, and negative growth rates in both time series closely corresponded. This further supported the interpretation of this mode of variability as describing age group 1 growth rates. As will be expanded upon in the following section, the lack of linkage between growth rates in age group 1 and the other age groups is likely related to the fact that *S. diploproa* inhabits an environment during the first year of life that is quite different from that during later states of life (Boehlert 1977) and is thus subject to different environmental factors influencing growth rates.

As with *S. pinniger*, the third principal component of *S. diploproa* growth rates has no obvious physical interpretation. The loading values (Fig. 5B) oscillate from positive to negative across the age groups, and the principal component time series (Fig. 7) was nearly normal over the entire record length.

DISCUSSION

The study of growth in marine fishes has typically been concerned with relatively short-term trends in growth of cohorts or populations, most often with fished stocks. Differences in growth may have existed between stocks (Templeman and Squires 1956; Borisov 1979), geographical regions (Boehlert and Kappenman 1980), stock densities, and years (Margetts and Holt 1948; Jones 1983). Such growth differences may be due to genetic factors (Borisov 1979), density dependence (Margetts and Holt 1948; Peterman and Bradford 1987), or environmental factors, most importantly temperature (Brett 1979; Kreuz et al. 1982). The dramatic reduction in stock sizes of many *Sebastes* spp. (Archibald et al. 1983; Ito et al. 1987) has led several authors to suggest density-dependent increases in growth (Gunderson 1977; Boehlert and Kappenman 1980). Recent changes in ageing methodology for *Sebastes* (Boehlert and Yoklavich 1984), however, have rendered long-term comparisons of growth difficult without a historical collection of otoliths.

Analogous to historical time series derived from tree rings (Fritts 1976), the technique described in our paper uses uniform methodology to develop time series of growth for long-lived fishes. Reading of otoliths, however, has more inherent variability than that for tree rings, and the resultant ageing biases described earlier must be considered. The impacts of ageing errors will be most apparent in high frequency signals in the time series and are probably not well resolved by our data; this is the main reason we used the running averages to low-pass filter the data, making the low frequency signals more apparent to the human eye (Figs. 3, 4, 6, 7).

An interesting biological feature of our results is the differing pattern of growth of age group 1 *S. diploproa* (Fig. 4), the only age group not contributing significantly to the variance described by the first principal component for either species. In contrast, first year growth in *S. pinniger* was similar to that in age groups 2–6. *Sebastes pinniger* have a relatively narrow seasonal spawning peak (Westrheim 1975; Gunderson et al. 1980), and pelagic young apparently recruited to their juvenile benthic habitats within about 6 months (Richardson and Laroche 1979). *Sebastes diploproa*, however, seemed to spawn during most months of the year (Snytko 1975), and pelagic prejuveniles were present year-round, at least in the Southern California Bight (Boehlert 1977). Assuming that the first annulus is laid down on a seasonal basis, first year growth was probably quite variable. Further, *S. diploproa* are deepwater (200–500 m) members of this genus, but their first year is spent in surface waters, probably in the upper meter of the water column (Boehlert 1977, 1981); thus, the factors influencing growth in the first year may differ from those affecting growth in subsequent years. Temperature can have an important impact on juvenile rockfish growth (see summary in Boehlert and Yoklavich (1983)), but it may not show coherent cycles between deep and shallow water over the continental shelf off Oregon (Kruse and Huyer 1983); thus, differences between growth rates for age group 1 and later age groups are not surprising.

The dominant signal apparent in all of the time series of growth, except age group 1 of *S. diploproa* (Figs. 3, 4), and in the first principal component for both species (Figs. 6, 7) was that of increased growth after about 1972. Many of the fish used to calculate the growth anomaly values for this period would have been captured before the age at full recruitment to the fishery, which is 12 years for *S. pinniger* (Wilson 1985) and 14 years for *S. diploproa* (Boehlert 1980). A potential concern with the use of fish younger than the age at full recruitment is that the gear will be selective for larger, faster growing individuals; thus, fish younger than the age at full recruitment might conceivably be characterized by more rapid growth rates, resulting in the increased growth rates observed late in the time series (Figs. 3, 4). If true, then the size of growth increments for fish born in a given year should decrease with time from first recruitment until the age at full recruitment (as is true in Lee's phenomenon). Our samples, however, were taken with sampling gear of much smaller mesh than used in the commercial fishery (Gunderson and Sample 1980). Nonetheless, to test for more rapid growth of younger age fish, we compared the six growth indexes of *S. pinniger* born in 1973–77 and collected in 1980 (N = 41, ages 3–7) with those collected in 1984 (N = 51, ages 7–11). This timespan covered the most rapid increase in growth (Figs. 3, 4). The growth indexes did not significantly differ (paired t-test, $P > 0.10$); this suggests that the size of growth increments did not change as fish born in 1973–77 were collected 4 years closer to the age at full recruitment (1984 versus 1980).

An alternative explanation of increased growth in the 1970's was density dependence. Density-dependent growth has been observed in a variety of fish stocks, generally in association with exploitation (Margetts and Holt 1948) or strong year classes (Jones 1983), and is most evident in immature fish (see summary in Ware (1980)). There is little question that stocks of several *Sebastes* spp. have declined under the influence of fisheries (Gunderson 1984; Bracken 1987; Lenarz 1987; Westrheim 1987). Ito et al. (1987) have suggested that stocks of *S. alutus* off Oregon, Washington, and British Columbia declined from a virgin biomass of about 144,000 metric tons (t) to about 13,500 t in the early 1970's. No direct work documents density-dependent changes in growth in this species, although Gunderson's (1977) model of the stock used increased growth as a compensatory mechanism at low stock density. The best evidence for density-dependent growth changes in the genus is for *S. mentella* (Sorokin et al. 1986). For *S. diploproa*, length frequencies from 1977 (Boehlert 1980) were shifted to much smaller sizes than those from 1961 to 1962 (Alverson et al. 1964); this decrease may have been a result of fishing pressure (Boehlert 1980). Faster growth in the region north of California has been described for this species (Boehlert and Kappenman 1980); density-dependent growth increase (since the major stock reduction occurred in the north) was suggested as one of the factors responsible for the geographical growth differences.

The decrease in stock size of many deepwater *Sebastes* spp. along the west coast of North America and the Gulf of Alaska may be related to the growth increase after about 1972 for both species. The major removals of this group by foreign fisheries occurred in the mid-1960's to 1970's (Bracken 1987; Ito et al. 1987; Westrheim 1987). Time series of reliable biomass estimates for *S. pinniger* and *S. diploproa* are not available, but estimates for *S. alutus* have been made using the stock reduction analysis method (Ito et al. 1987). All three species inhabit similar environments and depend upon similar food resources, so biomass estimates for *S. alutus* can be used as a proxy of biomass for the other two species. A comparison of the first principal component time series of *S. pinniger* and *S. diploproa* with the stock size of *S. alutus* on the west coast (Ito et al. 1987) shows that the increase in growth begins slightly after the major stock decline (Fig. 8). The stock size of *S. alutus* is negatively correlated with the first principal component (and thus growth indexes) for both species ($P < 0.01$).

If decreased stock size is responsible for the increased growth evident in both species, it apparently occurs in age groups 1–6 for *S. pinniger* (Figs. 3, 5A) and in age groups 2–6 for *S. diploproa* (Figs. 4, 5B). The ecological differences between age group 1 and older *S. diploproa* (described above) may explain why density-dependent growth does not occur in the young fish. Density-dependent growth in the first year of life has been described for several fishes (van der Veer 1986; Peterman and Bradford 1987) that

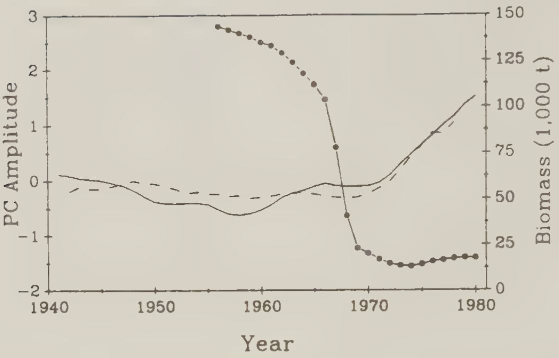


FIGURE 8.—Comparison of the smoothed first principal component time series of *Sebastes pinniger* (dashed line) and *S. diploproa* (solid line) with data on the stock size of *S. alutus* (circles) from Oregon, Washington, and British Columbia (Ito et al. 1987).

typically have a limiting juvenile habitat (often estuarine) and a much more extensive adult habitat. Indeed, Peterman and Bradford (1987) have suggested that density-dependent growth of English sole, *Parophrys vetulus*, off the coast of Oregon occurs only in the first year of life but not later. In *S. diploproa*, the opposite occurs. The adult habitat is restricted bathymetrically and latitudinally, whereas the pelagic prejuveniles occur in a very extensive epipelagic habitat subject to different environmental factors, competitors, and food resources. It is doubtful that variations in density of *Sebastes* in this habitat would impact growth significantly. In the adult habitat of both *S. pinniger* and *S. diploproa*, however, the immense virgin biomass of members of this genus has been reduced significantly. Further, most rockfish species commercially exploited by the trawl fishery rely on the same food resource, with euphausids as the principal prey (Phillips 1964; Brodeur and Pearcy 1984). The increased availability of prey resources associated with stock decline could conceivably result in increased growth in most species. Snytko and Fedorov (1974) suggested that some rockfish species have increased their geographic ranges at the expense of the decreased stocks of *S. alutus*; density-dependent growth could be a corollary of such a range extension.

The nonstationary characteristic due to the sudden increases in growth late in the time series makes correlations of growth indexes with environmental factors difficult to evaluate. Further, sea level, wind stress curl, and the first principal component time series of *S. diploproa* and *S. pinniger* were all serially correlated in the 1946–77 data base, indicating temporal trends that decrease the number of independent degrees of freedom in the sample correlation estimates and that introduce potentially spurious correlations (Chelton 1983, 1984; Bakun 1985). Correlations of the relationship of growth data to time series of physical factors (sea level, sea-surface temperature, upwelling index, and wind stress curl) were determined (Table 1); the 95% significance levels were calculated using the formula in Chelton (1983), which accounts for the reduced number of degrees of freedom from serial correlations. For *S. pinniger*, a significant, positive correlation existed between the second principal component and both the April-September upwelling index and sea level (Table 1); a significant, positive correlation also existed between both growth for age group 6 (G6 in Table 1) and the second principal component with the April-September upwelling index for the prior year. Growth in age group 6 contributed significantly to the variance described by the second principal component (Fig. 5A), so the similarity was not surprising. Feeding by *S. pinniger* increased during the spring-summer upwelling period when *Euphausia pacifica* was the dominant diet item and the frequency of empty stomachs was lower (Brodeur and Pearcy 1984). This must also be the time that fat deposition occurs in this species since the peak fat content was in fall (Guillemot et al. 1985). The effects of upwelling in a prior year on growth may be related to delayed growth using the energy from stored fat reserves built up during the prior upwelling season. The importance of upwelling in rockfish feeding is shown by the decreased fat storage in El Niño years in *S. flavidus* (Lenarz and Echeverria 1986).

For *S. diploproa*, wind stress curl was negatively correlated with the growth indexes for age groups 2, 4, and 6, with mean growth for age groups 2–6 (G26), and with the first principal component (Table 1), which reflects most closely growth from ages 2–6 (Fig. 5B). Negative wind stress curl is associated with offshore convergence (Nelson 1977), which could concentrate prey (such as euphausids) and potentially increase feeding efficiency during the spring-summer upwelling season when maximum feeding takes place. Sea-surface temperature is negatively correlated with growth in year 2, whereas it is positively (but nonsignificantly) correlated with growth in year 1; the correlation between the second principal component (which reflects growth in year 1) and sea-surface temperature is significant, however, suggesting a real difference between the response of these age groups to temperature. This difference may be involved with an ontogenetic shift in the temperature for optimum growth for this species as noted by Boehlert (1981).

TABLE 1.—Pearson correlation matrices for six age group growth indexes (G1–6), mean growth indexes (G for *Sebastes pinniger*, G26 for *S. diploproa*), and principal component time series of the three dominant modes of variability (PC 1–3) with environmental factors from 1946 to 1977; mean yearly values (as opposed to smoothed values) are used in these calculations. The mean growth index for *S. diploproa* is for ages 2–6 because of differences in growth in age group 1. The significance levels of coefficients were calculated following Chelton (1983). CURL, wind stress curl at lat. 45°N, long. 125°W; UP, yearly average Bakun upwelling index at lat. 45°N; SSTNB, sea-surface temperature at Neah Bay, WA; UP49, upwelling index averaged for April–September; and SLSF, sea level at San Francisco.

Index	CURL	UP	SSTNB	UP49	SLSF
S. pinniger					
G1	−0.288	0.105	−0.254	0.163	−0.033
G2	0.065	−0.057	−0.032	−0.165	−0.236
G3	0.049	−0.296	−0.078	−0.261	−0.344
G4	−0.058	0.205	−0.173	−0.013	−0.182
G5	−0.066	0.162	−0.140	0.344	0.083
G6	−0.500	0.123	−0.088	0.274	0.429
G	−0.262	0.085	−0.243	0.127	−0.069
PC 1	−0.228	0.077	−0.247	0.109	−0.113
PC 2	−0.344	0.192	−0.061	0.416*	0.459*
PC 3	−0.178	0.261	−0.091	0.081	0.089
S. diploproa					
G1	0.007	0.034	0.363	−0.079	0.075
G2	−0.567*	−0.122	−0.351*	−0.025	−0.041
G3	−0.270	0.127	−0.072	0.062	0.277
G4	−0.453*	−0.392*	0.267	−0.326	−0.140
G5	−0.310	−0.024	−0.293	0.200	−0.216
G6	−0.349*	−0.056	−0.094	0.021	−0.350
G26	−0.619*	−0.163	−0.148	−0.027	−0.120
PC 1	−0.635*	−0.172	−0.145	−0.044	−0.130
PC 2	0.032	0.016	0.438*	−0.126	0.229
PC 3	−0.092	0.029	−0.175	0.200	−0.239

* = $P < 0.05$

With the exception of the correlations noted above, the general lack of strong relationships of fish growth with physical parameters may be due to several causes. First, errors in methodology may cause lower resolution in the growth time series than would be necessary to demonstrate the associations. Second, the complexity of factors having an impact upon fish growth (Weatherley 1976; Brett 1979) makes detecting relationships of growth with individual physical factors difficult; furthermore, fish growth may be related to environmental factors in a nonlinear fashion. Higher resolution in the measuring technique and minimization of ageing errors will be necessary to address the first of these problems. The second problem can be addressed through nonlinear analysis of the relationships and continuation of the time series of growth anomalies, which will help define the relationships of growth with physical and biological factors.

CONCLUSION

The research we describe develops a new technique for constructing historical time series of fish growth and conducts analysis into the causes of growth variation in *Sebastes diploproa* and *S. pinniger*. The technique is applicable to a variety of marine organisms for which chronographic records are deposited in some calcareous structures. Our analysis of the record for *S. diploproa* and *S. pinniger* is characterized by a strong signal of increased growth late in the record. Although this signal is confounded by questions associated with size-selective mortality and Lee's phenomenon, we interpret it to indicate a density-dependent response to stocks depleted by overfishing. Our interpretation can be tested; if stocks of *Sebastes* are allowed to rebuild, the dominant signal of increased growth evident in the time series (Figs. 3, 4, 6, 7) should return to more normal values. We recommend that these time series be continued and that the techniques be applied to other species. The interrelationships among species and further investigation of the role of environmental factors in annual fish growth variation could provide valuable insights into population responses of fishes to their physical and biological environment.

ACKNOWLEDGMENTS

This research was conducted at the Oregon State University Marine Science Center, Newport, OR. We acknowledge funding for this project from the Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, under Contracts 81-ABC-00192, 40ABNF-5-262, and NA-85ABH-00025 and the National Science Foundation under Grant OCE-8315421. We thank C. D. Wilson for technical assistance; W. G. Pearcy for discussions; and A. Bakun, B. Leaman, S. Ralston, and D. Somerton for critical reviews of earlier drafts.

LITERATURE CITED

Alverson, D. L., A. T. Pruter, and L. L. Ronholt.
1964. A study of demersal fishes and fisheries of the northeastern Pacific Ocean. H. R. MacMillan Lectures in Fisheries. Inst. Fish., Univ. Br. Columbia, Vancouver, B.C., 190 p.

Archibald, C. P., D. Fournier, and B. M. Leaman.
1983. Reconstruction of stock history and development of rehabilitation strategies for Pacific ocean perch in Queen Charlotte Sound, Canada. N. Am. J. Fish. Manage. 3:283–294.

Archibald, C. P., W. Shaw, and B. M. Leaman.
1981. Growth and mortality estimates of rockfishes (Scorpaenidae) from B.C. coastal waters, 1977–1979. Can. Tech. Rep. Fish. Aquat. Sci. 1048, 57 p.

Bakun, A.
1985. Comparative studies and the recruitment problem: Searching for generalizations. Calif. Coop. Oceanic Fish. Invest. Rep. 26:30–40.

Bennett, J. T., G. W. Boehlert, and K. K. Turekian.
1982. Confirmation of longevity in *Sebastes diploproa* (Pisces: Scorpaenidae) using 210Pb/226Ra measurements in otoliths. Mar. Biol. (Berl.) 71:209–215.

Boehlert, G. W.
1977. Timing of the surface-to-benthic migration in juvenile rockfish, *Sebastes diploproa*, off southern California. Fish. Bull., U.S. 75:887–890.
1980. Size composition, age composition, and growth of canary rockfish (*Sebastes pinniger*) from the 1977 rockfish survey. Mar. Fish. Rev. 42(3–4):57–63.
1981. The effects of photoperiod and temperature on laboratory growth of juvenile *Sebastes diploproa* and a comparison with growth in the field. Fish. Bull., U.S. 79:789–794.
1985. Using objective criteria and multiple regression models for age determination in fishes. Fish. Bull., U.S. 83:103–117.

Boehlert, G. W., and R. F. Kappenman.
1980. Variation of growth with latitude in two species of rockfish (*Sebastes pinniger* and *S. diploproa*) from the northeast Pacific Ocean. Mar. Ecol. Prog. Ser. 3:1–10.

Boehlert, G. W., and M. M. Yoklavich.
1983. Effects of temperature, ration, and fish size ongrowth of juvenile black rockfish, *Sebastes melanops*. Environ. Biol. Fishes 8:17–28.
1984. Variability in age estimates in *Sebastes* as a function of methodology, different readers, and different laboratories. Calif. Fish Game 70:210–224.
1987. Long-term cycles of growth in *Sebastes*: extracting information from otoliths. *In* Proceedings of the International Rockfish Symposium, p. 197–207. Alaska Sea Grant Rep. 87-2, Anchorage, AK.

Borisov, V. M.
1979. The selective effect of fishing on the population of species with a long life cycle. J. Ichthyol. 18:896–904. (Engl. transl. Vopr-Ikhtiol.)

Bracken, B.
1987. The history of the rockfish fisheries in Alaskan waters. *In* Proceedings of the International Rockfish Symposium, p. 51–59. Alaska Sea Grant Rep. 87-2, Anchorage, AK.

Brett, J. R.
1979. Environmental factors and growth. *In* W. S. Hoar, D. J. Randall, and J. R. Brett (editors), Fish physiology. Vol. VIII. Bioenergetics and growth, p. 599–677. Acad. Press, N.Y.

Brodeur, R. D., and W. G. Pearcy.
1984. Food habits and dietary overlap of some shelf rockfishes (genus *Sebastes*) from the northeastern Pacific Ocean. Fish. Bull., U.S. 82:269–294.

Campana, S. E., and J. D. Neilson.
1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42:1014–1032.

Chelton, D. B.
1983. Effects of sampling errors in statistical estimation. Deep-Sea Res. 30:1083–1103.
1984. Commentary: Short-term climatic variability in the northeast Pacific Ocean. *In* W. G. Pearcy (editor), The influence of ocean conditions on the production of salmonids in the North Pacific, p. 87–99. Oregon State Univ., Sea Grant ORESU-W-83-001.

Cushing, D. H.
1982. Climate and fisheries. Acad. Press, N.Y., 373 p.

Favro, L. D., P. K. Kuo, and J. F. MacDonald.
1979. Population-genetic study of the effects of selective fishing on the growth rate of trout. J. Fish. Res. Board Can. 36:552–561.

Fritts, H. C.
1976. Tree rings and climate. Acad. Press, N.Y., 567 p.

Guillemot, P. J., R. J. Larson, and W. H. Lenarz.
1985. Seasonal cycles of fat and gonad volume in five species of northern California rockfish (Scorpaenidae: *Sebastes*). Fish. Bull., U.S. 83:299–311.

Gunderson, D. R.
1977. Population biology of Pacific ocean perch, *Sebastes alutus*, stocks in the Washington-Queen Charlotte sound region, and their response to fishing. Fish. Bull., U.S. 75:369–403.
1984. The great widow rockfish hunt of 1980–1982. N. Am. J. Fish. Manage. 4:465–468.

Gunderson, D. R., P. Callahan, and B. Goiney.
1980. Maturation and fecundity of four species of *Sebastes*. Mar. Fish. Rev. 42(3–4):74–79.

Gunderson, D. R., and T. M. Sample
1980. Distribution and abundance of rockfish off Washington, Oregon, and California during 1977. Mar. Fish. Rev. 42(3–4):2–16.

Harris, G. P., P. Davies, M. Nunez, and G. Meyers.
1988. Interannual variability in climate and fisheries in Tasmania. Nature 333:754–757.

Hotelling, H.
1933. Analysis of a complex of statistical variables into principal components. J. Ed. Psychol. 24:417–441, 489–520.

Ito, D. H., D. K. Kimura, and M. E. Wilkins.
1987. Status and future prospects for the Pacific ocean perch resource in waters off Washington and Oregon as assessed in 1986. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-NWC-113, 50 p.

Jones, R.
1983. An investigation of North Sea haddock (*Melanogrammus aeglefinus*) length-at-age data, with particular reference to the effects on growth of the outstanding year classes of 1962 and 1967. J. Cons., Cons. int. Explor. Mer 41:50–62.

Kreuz, K. F., A. V. Tyler, G. H. Kruse, and R. L. Demory.
1982. Variation in growth of Dover soles and English soles as related to upwelling. Trans. Am. Fish. Soc. 111:180–192.

Kruse, G. H., and A. Huyer.
1983. Relationships among shelf temperatures, coastal sea level, and the coastal upwelling index off Newport, Oregon. Can. J. Fish. Aquat. Sci. 40:238–242.

Leaman, B. M., and R. J. Beamish.
1984. Ecological and management implications of longevity in some northeast Pacific groundfishes. Int. North Pac. Fish. Comm., Bull. 42:85–97.

Leaman, B. M., and D. A. Nagtegaal.
1987. Age validation and revised natural mortality rate for yellowtail rockfish. Trans. Am. Fish. Soc. 116:171–175.

Lenarz, W.
1987. A history of California rockfish fisheries. *In* Proceedings of the International Rockfish Symposium, p. 35–41. Alaska Sea Grant Rep. 87-2, Anchorage, AK.

Lenarz, W. H., and T. W. Echeverria.
1986. Comparison of visceral fat and gonadal fat volumes of yellowtail rockfish, *Sebastes flavidus*, during a normal year and a year of El Niño conditions. Fish. Bull., U.S. 84:743–745.

Loeb, V. J., P. E. Smith, and H. G. Moser.
1983. Recurrent groups of larval fish species in the California Current area. Calif. Coop. Oceanic Fish. Invest. Rep. 23:152–164.

Margetts, A. R., and S. J. Holt.
1948. The effect of the 1939–1945 war on the English North Sea trawl fisheries. Rapp. P.-v Reun. Cons. int. Explor. Mer 122:26–46.

Moser, H. G., P. E. Smith, and L. E. Eber.
1987. Larval fish assemblages in the California Current region, 1954–1960, a period of dynamic environmental change. Calif. Coop. Oceanic Fish. Invest. Rep. 28:97–127.

Mulcahy, S. A., J. S. Killingley, C. F. Phleger, and W. H. Berger.
1979. Isotopic composition of otoliths from a benthopelagic fish, *Coryphaenoides acrolepis*, Macrouridae: Gadiformes. Oceanol. Acta 2:423–427.

Mulligan, T. J., F. D. Martin, R. A. Smucker, and D. A. Wright.
1987. A method of stock identification based on the elemental composition of striped bass *Morone saxatilis* (Walbaum) otoliths. J. exp. mar. Biol. Ecol. 114:241–248.

Mysak, L. A., W. W. Hsieh, and T. R. Parsons.
1982. On the relationship between interannual baroclinic waves and fish populations in the northeast Pacific. Biol. Oceanogr. 2:63–103.

Nelson, C. S.
1977. Wind stress and wind stress curl over the California Current. U.S. Dep. Commer., NOAA Tech. Rep. NMFS, SSRF-714, 87 p.

Peterman, R. M., and M. J. Bradford.
1987. Density-dependent growth of age 1 English sole (*Parophrys vetulus*) in Oregon and Washington coastal waters. Can. J. Fish. Aquat. Sci. 44:48–53.

Phillips, J. B.
1964. Life history studies on ten species of rockfish (genus *Sebastodes*). Calif. Dep. Fish Game, Fish Bull. 126, 70 p.

Radtke, R. L.
1984. Cod fish otoliths: Information storage structures. *In* E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal (editors), The propagation of cod *Gadus morhua* L., p. 273–298. Flødevigen Rapp., Vol. 1.
1987. Age and growth information available from the otoliths of the Hawaiian snapper, *Pristipomoides filamentosus*. Coral Reefs 6:19–25.

Richardson, S. L., and W. A. Laroche.
1979. Development and occurrence of larvae and juveniles of the rockfishes *Sebastes crameri*, *Sebastes pinniger*, and *Sebastes helvomaculatus* (Family: Scorpaenidae) off Oregon. Fish. Bull., U.S. 77:1–46.

Ricker, W. E.
1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production, and yield. J. Fish. Res. Board Can. 26:479–541.

Rogers, D. E.
1984. Trends in abundance of northeastern Pacific stocks of salmon. *In* W. G. Pearcy (editor), The influence of ocean conditions on the production of salmonids in the North Pacific, p. 100–127. Oregon State Univ. Sea Grant, ORESU-W-83-001.

Shackleton, L. Y.
1987. A comparative study of fossil fish scales from three upwelling regions. *In* A. I. Payne, J. A. Land, and K. H. Brink (editors), The Benguela and comparable ecosystems, Vol. 5, p. 79–84. S. Afr. J. Mar. Sci.

Snytko, V. A.
1975. New data on distribution of the splitnose rockfish *Sebastes diploproa* (Gilbert 1890) and some notes on its biology. [In Russ.] Izv. TINRO 96:291–293, Vladivostok.

Snytko, V. A., and V. V. Fedorov.
1974. New data on the distribution of scorpaenid fishes of the subfamily Sebastinae and notes on their biology. J. Ichthyol. 14:811–818. (Engl. transl. Vopr-Ikhtiol.)

Sorokin, V. P., L. M. Shestova, and E. G. Lukmanov.
1986. Growth and maturity of the Norwegian-Barents Sea stock redfish *Sebastes mentella* in 1966–1972 and 1975–1983. Int. Counc. Explor. Sea C.M. 1986/G:24, Demersal Fish Committee, Sess. Q., 26 p.

Soutar, A., and J. D. Isaacs.
1974. Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment off the Californias. Fish. Bull., U.S. 72:257–273.

Templeman, W., and H. J. Squires.
1956. Relation of otolith lengths and weights in the haddock *Melanogrammus aeglefinis* (L.) to the rate of growth of the fish. J. Fish. Res. Board Can. 13:467–487.

van der Veer, H. W.
1986. Immigration, settlement, and density-dependent mortality of a larval and early postlarval 0-group plaice (*Pleuronectes platessa*) population in the western Wadden Sea. Mar. Ecol. Prog. Ser. 29:223–236.

Ware, D. M.
1980. Bioenergetics of stock and recruitment. Can. J. Fish. Aquat. Sci. 37:1012–1024.

Weatherley, A. H.
1976. Factors affecting maximization of fish growth. J. Fish. Res. Board Can. 33:1046–1058.

Westrheim, S. J.
1975. Reproduction, maturation, and identification of larvae of some *Sebastes* (Scorpaenidae) species in the northeast Pacific Ocean. J. Fish. Res. Board Can. 32:2399–2411.

1987. The rockfish fisheries off western Canada, 1860–1985. *In* Proceedings of the International Rockfish Symposium, p. 43–50. Alaska Sea Grant Rep. 87-2, Anchorage, AK.

Wilson, C. D.
1985. The effects of different otolith ageing techniques on estimates of growth and mortality for two species of rockfishes, *Sebastes pinniger* and *Sebastes diploproa*. M.S. Thesis, Oregon State Univ., Corvallis, OR, 107 p.

Wolfe, D. A., M. A. Champ, D. A. Flemer, and A. J. Mearns.
1987. Long-term biological data sets: Their role in research, monitoring, and management of estuarine and coastal marine systems. Estuaries 10:181–193.

8910

Vital Rate Statistics for Billfish Stock Assessment

Christofer H. Boggs

Growth, mortality, recruitment, and migration rates are sometimes called "vital" statistics because they are "life" history parameters used in population dynamics models. Since the previous symposium (Shomura and Williams 1974, 1975) and the Pacific billfish workshop in 1977 (Shomura 1980), many studies have been conducted on billfish vital rates, concentrating mostly on age and growth rates. Analysis of hardpart markings has advanced growth rate estimation beyond the old method of following length-frequency modes through time. Billfish stock assessments making use of age and growth data have, however, been limited to western Atlantic stocks of swordfish *(Xiphias gladius)* and Atlantic sailfish *(Istiophorus albicans)* (Conser 1984, SEFC 1987). Much of the available data on billfish vital rates have not been utilized. This chapter compares some new vital rate estimates with older ones and examines their adequacy for stock assessment.

Growth Rates

Methods of Estimating Growth

All approaches to estimating growth have major limitations, as applied to billfish. These limitations must be addressed because different approaches (Table 1) have not produced similar results. Analysis of length-frequency modes has been applied to most species. This method is relatively easy, but it depends on assumptions not met for most billfish. Length-frequency modes do not represent age classes unless the spawning season is distinct, no mixing occurs for fish with different growth rates or from different spawning seasons, and the length sampling process is not selective. Each sequential length-frequency sample must be collected over a short time frame, or growth will blur the modes. When these conditions are met, growth rate estimates are specific to the size of the modes analyzed, but actual age is still not known. To construct a growth curve showing growth as a function of age (e.g., Atlantic swordfish, Fig. 1), it is necessary to assume that the mode for the smallest fish represents a given age (in this case, 1 year old). An additional problem with constructing growth models from length-frequency data is that, as growth slows with age, the modes becomes indistinguishable.

The tag-and-recapture method of estimating growth is compromised by the lack of age determinations or precise sizes of billfish at tagging. Estimates of change in size divided by time since tagging and release provide growth rates for specific sizes of fish that can be useful in verifying results from other methods (Conser 1984). Unfortunately, the weight at tagging is often estimated visually, so individual growth estimates are often wrong and frequently negative (SEFC 1987). The justification for the method is that, on average, no systematic bias exists in the estimated weight at release. As more tournaments encourage the tagging and release of billfish, promoting better methods of estimating initial size might be advantageous. Such methods could include the use of measured streamers, slipped onto the leader to trail alongside the fish, and photography. The remaining problem is that age is not known. Fitting an age-specific growth model to tag-and-recapture growth data requires assumptions about age and assumptions about how growth rate changes with age (the form of the model). For example, for Atlantic swordfish (Fig. 1), a model was used that assumed an increasing growth rate phase early in life and a diminishing growth rate phase later in life (Gompertz model: SEFC 1987). It was also assumed that age 0 fish were 1.4 kg (3 lb) dressed weight.

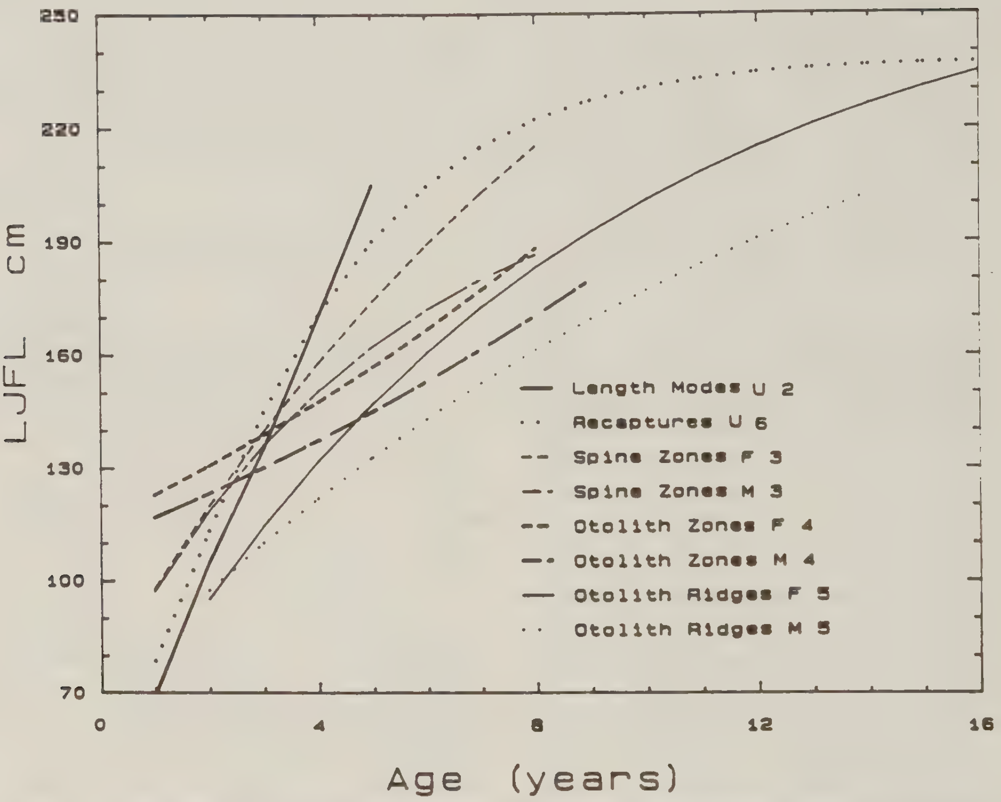


Figure 1. Length (LJFL = lower jaw to fork length) versus age curves for swordfish *(Xiphias gladius)*. Numerals in the key refer to literature in footnote 3 of Table 1. M = male, F = female, and U = unknown or unreported.

Biologists have been reluctant to use age-specific growth rate models based on billfish hardpart studies because of a lack of verification and a near absence of validation. Verification is agreement between age estimates from one method, or source of material (i.e., hard parts), and those from another. Validation is proof that a count of hardpart markings equals the measured passage of time (i.e., time since hatching or since the hard parts were chemically marked). Thorough validation is proof that, throughout the life of the animal, hardpart markings are deposited at regular intervals (i.e., one per day or per year). Marginal increment studies to establish the periodicity of growth mark formation on billfish hard parts have not yet produced definitive results (Berkeley and Houde 1983, Prince et al 1987). Failed attempts to verify billfish hardpart age estimates have usually involved counts of large-scale internal zones observed in spines compared with some other hardpart estimate (Radtke and Hurley 1983, Prince et al 1986, 1987). Spine zone counting is popular because spines are easily removed and cause little damage to marketable fish, but spines contain living tissue that can resorb inner zones. A method of estimating missing zones based on spine diameter appears to resolve this discrepancy (Hill 1986). Verification has been obtained by using fine-scale increment counts across the entire radius of otoliths for two adult swordfish, aged 6 and 9 years old based on external otolith ridge counts (Radtke and Hurley 1983). The daily addition of fine-scale increments in otoliths has been validated in many tropical species, including yellowfin tuna *(Thunnus albacares)* (Wild and Foreman 1980). So, although extremely small and difficult to remove, billfish otoliths are useful indicators of age.

A few good validations of annual marks or daily fine-scale increments in billfish hard parts could remove much of the skepticism that has kept a large amount of age and growth research (Table 1) from being applied to stock assessment. The reluctance to apply growth curves based on hardpart aging data is not appropriate, considering that growth curves based on other approaches which have been applied are equally unproven. There is a single validation of a billfish age estimate: An Atlantic sailfish recaptured 10.8 years after being tagged as a 2- to 4-year old had 13 external otolith ridges (Prince et al 1986). Validation in billfish hardpart aging

Table 1. Billfish growth and mortality rate estimates. Von Bertalanffy growth parameters were taken directly from the literature or from analyses of data therein (see Shomura 1980). Natural mortality rates (M) were calculated from K using the equation of Murphy and Sakagawa (1977).

Locality	Method	No.	Sex[1]	Size range[2] (cm)	Source[3]	Growth parameters			M
						K	t_0	L_∞	
				Swordfish					
Pacific	Length modes		U	61-245	1	0.124	-1.169	309 cm	0.22
Atlantic	Length modes and vertebrae		U	50-260	2	[4]0.230		[4]365 cm	0.43
	Anal spine	275	M	70-270	3	0.19	-2.04	217 cm	0.35
	internal zones	164	F			0.09	-2.59	340 cm	0.15
	Otolith	39	M	79-209	4				
	internal zones	39	F	102-290					
	Otolith ridges	73	M	88-208	5	0.07	-3.94	277 cm	0.12
		195	F	80-270		0.12	-1.68	267 cm	0.21
	Tag recapture	66	U	100-270	6				
				Pacific sailfish					
Pacific	Length modes	51,000	U	140-210	7	0.472		232 cm	0.90
				Atlantic sailfish					
Atlantic	Length modes	8,630	U	1-201	8	0.901	-0.496	243 cm	1.73
	Otolith ridges	64	U	102-184	9				
	Dorsal spine	259	M	80-186	10	0.301	-1.959	184 cm	0.56
	internal zones	310	F	86-198		0.159	-3.212	230 cm	0.29
	Tag recapture	59	U	100-180	11	Same as dorsal spines.[5]			
				Striped marlin					
Pacific	Length modes		U	120-235	12	0.264		275 cm	0.49
	Length modes	16,898	M	108-171	13	0.417	-0.521	206 cm	0.79
		13,532	F	108-175		0.696	0.136	186 cm	1.33
				Pacific blue marlin					
Pacific	Length modes	1,327	M	93-212	13	0.285	0.106	276 cm	0.53
		1,757	F	78-289		0.116	-0.161	505 cm	0.21
	Otolith ridges	7	M	165-191	14				
		7	F	217-294					
				Atlantic blue marlin					
Atlantic	Otolith ridges	8		87-136	15				
	Otolith and	10	M	82-157	16				
	dorsal spine	4	F	110-133					
	internal zones	6	U	82-140					
				Black marlin					
Pacific	Length modes		U	150-250	17	0.474		282 cm	0.90

[1] M = male, F = female, and U = unknown or unreported.

[2] Atlantic swordfish and Atlantic sailfish data are given in lower jaw fork length. All other data are given in eye to fork length. Transformations between size measurements are in Royce (1957) for Pacific marlin, Lenarz and Nakamura (1974) for Atlantic marlin, and Jolley (1977) for Atlantic sailfish.

[3] Sources: 1. Yabe et al. (1959), 2. Caddy (1976, 1977), 3. Berkeley and Houde (1983), 4. Wilson and Dean (1983), 5. Radtke and Hurley (1983), 6. SEFC (1987), 7. Koto and Kodama (1962a), 8. de Silva (1957), 9. Radtke and Dean (1981), 10. Hedgepeth and Jolley (1983), 11. Conser (1984), 12. Koto (1963), 13. Skillman and Yong (1976; all age groups, model 1), 14. Radtke (1983), 15. Radtke et al. (1982), 16. Prince et al. (1987), 17. Koto and Kodama (1962b).

[4] These estimates of K and L_∞ from Caddy (1977) do not match the size at age groups given in Caddy (1976). Midpoints of the age groups in Caddy (1976) were used to plot the curve in Figure 1.

[5] Conser (1984) refit the data of Hedgepeth and Jolley (1983) using nonlinear regression, and the results were much more similar between males ($K = 0.1947$, $t_0 = -3.168$, $L_\infty = 199.4$ cm, $M = 0.358$), and females ($K = 0.1967$, $t_0 = -2.842$, $L_\infty = 210.4$ cm, $M = 0.362$).

studies is extremely difficult because maintaining billfish of any age in the laboratory is not possible and injecting chemicals for marking hard parts is difficult during tagging. Newly available methods for injecting chemical markers into billfish from a distance with dart guns or syringes on the ends of sticks should help solve this problem.

Comparison of Growth Estimates

A difference in billfish growth rate by sex is usually seen when both sex and age are determined. Unfortunately, a lack of sex data for the catches makes it impossible to apply sex-specific growth curves in stock assessments (Conser 1984, SEFC 1987). The faster growth of females compared with males is clear in hardpart estimates for swordfish (Fig. 1) and Pacific blue marlin *(Makaira mazara)* (Fig. 2) but less distinct in Atlantic sailfish and in length-frequency mode estimates for Pacific blue marlin and striped marlin *(Tetrapturus audax)* (Table 1).

Growth rate differences between stocks within a species are not evident in a casual comparison of swordfish growth curves estimated from length-frequency mode data. After eye to fork length curves from the Pacific (Yabe et al 1959) and tropical Atlantic (Ovchinnikov et al 1980) are converted to lower jaw to fork length curves, they appear similiar to the data from the western Atlantic (Caddy 1976). Blue marlin age data from the Pacific, based on otolith ridge counts, barely overlap with data from the Atlantic (Fig. 2). Making comparisons between single growth parameters such as *K*, *to* and *Loo* can be misleading since they are not independent. The parameters are listed (Table 1) to update a previous summary (Shomura 1980), but comparisons are made between actual length at age estimates from the models (i.e., Figs. 1 and 2).

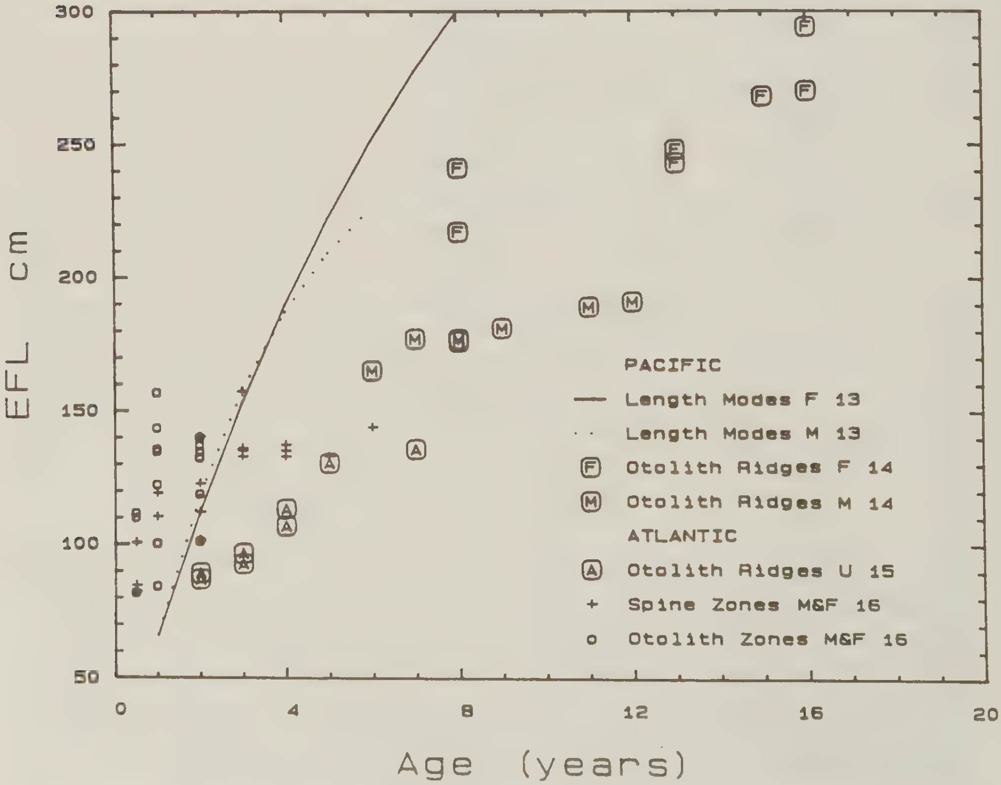


Figure 2. Length (EFL = eye to fork length) versus age data for Pacific blue marlin *(Makaira mazara)* and Atlantic blue marlin *(M. nigricans)*. Numerals in the key refer to literature in footnote 3 of Table 1. M = male, F = female, and U = unknown or unreported.

A comparison between Atlantic blue marlin *(M. nigricans)* and Pacific blue marlin is not a "stock" comparison since two separate species are now recognized (Nakamura 1985). Age-at-size estimates from Atlantic blue marlin otolith ridge counts barely overlap with those from Pacific blue marlin (Fig. 2).

Some of the discrepancies resulting from different approaches to estimating growth are too consistent to be due to true variation in the growth of the species caused by environmental and physiological variables (e.g., feeding, temperature, activity). Adult growth rates estimated from length-frequency mode analysis are always the fastest, and those from hard parts are always the slowest (Table 1), with tag-and-recapture estimates matching the length-frequency estimates in one case (swordfish; Fig. 1) and matching the hardpart estimates in another (Atlantic sailfish; Conser 1984). The slowest growth rates in adult swordfish (Fig. 1), Atlantic sailfish (Table 1), and Pacific blue marlin (Fig. 2) have been estimated from hard parts. The only validated datum (an Atlantic sailfish; Prince et al 1986) and the only study verified with complete fine-scale otolith increment counts (swordfish; Radtke and Hurley 1983) indicate that adult billfish are much older than estimated from other methods. In contrast to the slow growth in adult billfish indicated by hardpart studies, hardpart age estimates suggest that very young billfish grow much faster than indicated by other methods (Figs. 1 and 2).

Mortality Rates

Using Age and Growth Data

With growth curves (age-length relationships) and population length-frequency distributions, age-structured models can be used to estimate the proportion of fish being harvested, the annual variation in this proportion, and the effect on yield of changing the size of fish caught. However, even if growth curves are available, the inadequacy of data on length frequency, catch, and effort can prevent adequate stock assessments. Without vital rate statistics, analysis of catch and effort data can indicate only the level at which increasing fishing effort begins to produce a decrease in catch.

The most important application of growth models is the estimation of mortality rates which, in turn, are useful in determining sustainable yield. Total mortality *(Z)*, which is the rate of removal of fish from a population through fishing mortality *(F)* and natural mortality *(M)* combined $(F+M=Z)$, can be estimated from the age distribution in the population, as determined from the length-frequency distribution and a growth curve. With additional data on the catch, or with independent estimates of M, it is possible to separate F from M (Gulland 1983). As a rule of thumb,the level of catch may be sustainable if $F \ll M$, but the stock may be over-exploited if F is $\gg M$. Together or individually, fishing and natural mortality can remove more fish from the population in a year than are present at any given time. (F, M, or Z can be >1.0) if the population is constantly replacing biomass through recruitment and growth. In other words, a Z estimate of 1.5 means that 1.5 times the standing stock of fish die or are caught each year (under certain equilibrium conditions).

Estimating the average age of fish in the population is the simplest way to estimate Z, because the older all the fish are, the lower the mortality rate must be. The average age can be estimated from average age of the catch, adjusted by the age at first capture. Thus, Z can be estimated from the average length caught, adjusted by the size at first capture, using a growth curve to translate length into age. Other more complex procedures for estimating Z are based on the same idea (Gulland 1983). It is also possible to estimate Z from length-specific growth curves obtained from tag-recapture data and length-frequency data, without actually knowing true age (Wetherall et al 1987).

Adequate Accuracy and Precision

The accuracy of billfish age-length relationships is in doubt. How accurate do they need to be, and how much random error is acceptable? According to Powers (1983), who simulated the effects of bias and random error in assigning ages to length data, increasing lack of precision (random error) of up to 1 to 5% in assigning ages increases the standard error of Z estimates (in simulation), whereas increasing lack of precision in assigning age beyond 1 to 5% has only a slight effect on the standard error of Z estimates. Sample size (number of fish aged) has a much greater effect on the standard error of Z. Bias (inaccuracy) in assigning ages leads to a roughly equivalent opposite bias in Z.

The yield-per-recruit analysis for Atlantic sailfish by Conser (1984) is an example of the state of the art in age-structured billfish stock assessment: His Z estimates are from a variety of analytical methods applied to the same age and size-frequency data and cover a range equal to about 25% of the mean. This suggests biases no larger than those inherent in various analytical methods (25%) may be achieved with biases of up to about 25% in assigning ages, based on simulations in Powers (1983). Unfortunately, the disparity between ages given by various growth curves for billfish is often much greater than 100% (Table 1; Figs. 1 and 2). Thus, it is important to determine which growth models are correct.

Using Deterministic Growth Curves

Using a growth curve to assign ages by size results in assigning a single nonvariable age to a given length whereas, in reality, the ages of fish of a given size always vary. A biased age distribution results (Bartoo and Parker 1983). The worst case results when fish approach the asymptotic size given in the growth curve. In these slow-growing, older fish, size changes very little with age but does vary between individuals, so that many fish are actually larger than the theoretical maximum. These fish cannot be assigned an age by using a deterministic growth curve. Bartoo and Parker (1983) addressed this problem and recommended a stochastic method using estimated probabilities of various lengths at age. Unfortunately, this method was not used for either of the age-structured billfish stock assessments conducted to date.

Estimating Natural Mortality

Natural mortality *(M)* can be estimated from length-frequency data by using growth curves to assign age, as described above, but the length-frequency data must be from an unexploited population, i.e., when *F* is negligible and *Z* equals *M*. It is also possible to estimate *F* and *M* from tag-and-recapture data. However, data from unexploited populations or adequate tagging data are rarely available, so that models have been developed to estimate *M* directly from growth curve parameters (Murphy and Sakagawa 1977, Pauly 1980). The ideas supporting these models are that each species (or population or sex) has evolved growth and reproductive characteristics that balance a given *M*, providing the maximum possible reproductive success. Faster growth and reproduction have evolved in tandem with a high *M*. Slower growth and reproduction are more efficient when *M* is low. One model has included environmental temperature as a factor that increases *M* (Pauly 1980).

These models are poor substitutes for real information on natural mortality, which is almost completely lacking. However, Conser (1984) used both models (Murphy and Sakagawa 1977, Pauly 1980) and preexploitation length-frequency data on Atlantic sailfish to estimate *M* and found that all three were remarkably similar. I calculated a model estimate of *M* for each available von Bertalanffy *K* estimate (Table 1) using the model of Murphy and Sakagawa (1977). Pauly's (1980) method requires an estimate of asymptotic size (i.e., L_∞). Since length measures are problematic for billfish, the best choice would be asymptotic weight W_∞. Some estimate of the mean environmental temperature for each species would also be required.

Mortality Estimates and Stock Assessment

More age-structured billfish stock assessments are needed, and the two that were done should be reexamined in light of new growth rate estimates. For western Atlantic sailfish, Conser (1984) concluded that fishing mortality ($F = 0.338$), estimated from the difference between *Z* and *M*, was moderate and that the exploitation rate was sustainable. His yield-per-recruit analysis demonstrated that the size of fish being caught was larger than necessary to prevent growth overfishing. Conser (1984) used a growth curve based on dorsal spines (Hedgepeth and Jolley 1983) to estimate *Z* (0.674 from length-frequency distribution of the exploited stock) and *M* (0.336 from the pre-exploitation length-frequency distribution of the stock). Conser (1984) did not use an available growth curve based on otolith ridge counts (Radtke and Dean 1981). The otolith growth curve was not significantly different from the spine-based growth curve. The implications of the much greater estimate of Prince et al (1986) for sailfish longevity, however, based on a validated otolith ridge count, need to be examined.

Estimates of total mortality *(Z)* from tag recaptures can be used to check estimates derived from growth curves and length-frequency data. Decline in tag recovery rates over elapsed time since tagging is caused by *Z*. Tag-recovery *Z* estimates for western Atlantic sailfish (Conser 1984) ranged from 0.688 (corrected for tag shedding) to 1.11 (assuming no tag shedding). The corrected estimate was almost identical to the estimate used in the stock assessment (Conser 1984). Total mortality *(Z)* was estimated from tag recovery rate data on white marlin *(Tetrapturus albidus)* by Mather et al (1974), but no growth parameter estimates exist for comparison.

Age-structured stock assessments for marlins are nonexistent. Estimates of Z and M for striped marlin were given in Shomura (1980), who estimated $Z = 1.94$ (males) and $Z = 1.38$ (females) based on growth curves from Skillman and Yong (1976) and size-frequency data from the Hawaii longline fishery (Yoshida 1974). Assuming theoretical values for M (Table 1), I calculated F values of 1.15 (males) and 0.05 (females). These values seem unrealistic. The only mortality estimates for black marlin *(Makaira indica)*, or Atlantic or Pacific blue marlin are theoretical M estimates (Table 1).

The most elaborate age-structured billfish stock assessment to date was done on western Atlantic swordfish (SEFC 1987). "Virtual population analysis" (VPA) was used to estimate the number of fish present in past years, annual fishing mortality from the annual catch, and the annual number of survivors. The annual number of survivors can be estimated by working backwards, using an assumed constant M to estimate the fraction that died of natural causes each year and knowing the number caught each year. One must start with an estimate of the total number in the population, which can be calculated from M and the most recent catch by guessing the most recent annual value of F (terminal F). One also has to know the age distribution of the fish caught each year. Two "reasonable" estimates of M (0.1 and 0.2) used by SEFC (1987) were similar to theoretical M estimates based on K parameters from the otolith ridge count growth curves (Table 1). The growth curve used to age the catch was based on tag-and-recapture data and an assumed size at age 0 (Fig. 1).

The western Atlantic swordfish stock assessment workshop (SEFC 1987) concluded that the stock was not being overfished during 1982-1985. How would different assumptions about growth and mortality rates alter these conclusions? Recent estimates of growth rate are much slower than those used by SEFC (1987), which considered and rejected growth models based on spines (Berkeley and Houde 1983) and did not consider otolith ridge count estimates (Radtke and Hurley 1983). The growth curve based on dorsal spines was significantly different from the curve based on tag-and-recapture data. Consequently, workshop participants decided that, without validation, they could not use the spine data. What if the slower adult growth rate data (Fig. 1) are correct? Slower growth estimates produce lower theoretical M estimates (Table 1). An older population indicates a lower Z. This means the swordfish population would be replacing itself through growth and recruitment more slowly than SEFC (1987) suggests. What effect does a lower turnover rate have on estimates of F and the status of the swordfish stock? It is not necessary to wait until hardpart age estimates are validated to address this important question.

Other Vital Rate Statistics

Research on other vital rates such as migration, reproduction, and recruitment rates is extremely limited. Billfish migration rates have not been quantified, even though they confound estimates of mortality (SEFC 1987) and are critical for management. Instead, tag-and-recapture data have been used to describe qualitative movement patterns. The arrow diagram approach has been used to suggest segregation of stocks for assessment (SEFC 1987) and to explain seasonal changes in catch. However, without attention to the distribution of effort responsible for the recapture of tags, quantitative statements about movement are not possible from tagging data. Future tagging programs should make a concerted effort to monitor the fisheries involved in returning tags.

Miscellaneous information concerning size at maturity, fecundity, seasonality of reproduction, spawning areas, and larval distribution in billfish can be found in Shomura and Williams (1974,1975). The major use of such data for management purposes has been in separating stocks for assessment (e.g., SEFC 1987) rather than estimating reproductive rates or recruitment.

I was not able to find estimates of recruitment for any of the billfish except those resulting from the swordfish VPA in SEFC (1987). Such estimates result only from a concerted effort to analyze extensive size-frequency distribution data. The utility of recruitment rate estimates would be in estimating variation in productivity and in determining stock recruitment relationships in order to set minimal levels for the spawning stock. However, stock recruitment relationships are only one factor affecting recruitment. There is a need to understand the effects of environmental changes and species interactions on all of the vital rates. Current methods tend to assume that vital rates are constant.

Summary

The use of vital rate statistics such as growth and mortality rates in age-structured billfish stock assessments is a relatively recent development. Much work on growth rates has been accomplished recently, but only two age-structured billfish assessments have been made. The availability of size frequency data is a limiting factor. The implications of new estimates of growth rate based on hard parts have not been fully examined. Hardpart estimates suggest much older ages than do earlier studies based on analysis of length-frequency modes and growth of recaptured fish. Mortality estimates based on simulated length-frequency samples, using a growth curve to assign ages suggest that a large variance and considerable bias in age-at-size estimates result in acceptable levels of random error and comparable levels of bias. However, the discrepancies between results of different methods of estimating billfish growth are so large that mortality estimates based on the wrong growth model could be biased by ›100%. This level of accuracy is not acceptable. Slower growth and lower mortality rate estimates suggested by hardpart ageing studies indicate a slower turnover rate. The turnover rate is crucial in determining the amount of fishing the stock can sustain.

Age-structured stock assessment efforts have avoided using the most recent hardpart growth estimates because of a lack of validation or verification. Verification is being obtained through new techniques, but validation is extremely difficult for billfish. Increased attention to billfish tagging studies, resulting from the increased participation of sportfishermen, could help resolve the discrepancies between growth estimates. Techniques should be promoted to improve size estimation at tagging and to administer hardpart marking chemicals to validate growth rate estimates. However, it would not be wise to wait for hardpart age validation before examining the implications of much slower growth rates on the status of billfish stocks.

Literature Cited

Bartoo, N.W., and K.R. Parker. 1983. Stochastic age-frequency estimation using the von Bertalanffy growth equation. Fish. Bull., U.S. 81:91-96.

Berkeley, S.A., and E.D. Houde. 1983. Age determination of broadbill swordfish, *Xiphias gladius*, from the Straits of Florida, using anal fin spine sections. *In* E.D. Prince and L.M. Pulos (eds.), Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks. U.S. Dep. Commer. NOAA, Tech. Rep. NMFS 8:137-143.

Caddy, J.F. 1976. A review of some factors relevant to management of swordfish fisheries in the northwest Atlantic. Can. Fish. Mar. Serv. Tech. Rep. 633:36 p.

Caddy, J.F. 1977. Some approaches to elucidation of the dynamics of swordfish *(Xiphias gladius)* populations. Can. Fish. Mar. Serv. Tech. Rep. 1439:10 p.

Conser, R.J. 1984. Yield per recruit analysis of sailfish, *Istiophorus platypterus*, in the western Atlantic Ocean. Int. Comm. Conserv. Atl. Tunas Collect. Vol. Sci. Pap. 20(2):448-464.

de Silva, D.P. 1957. Studies on the age and growth of Atlantic sailfish, *Istiophorus americanus* (Cuvier), using length-frequency curves. Bull. Mar. Sci. Gulf. Carribb. 7(1-4):1-20.

Gulland, J.A. 1983, Fish stock assessment: A manual of basic methods. Vol. 1. John Wiley & Sons, N.Y.:223 p.

Hedgepeth, M.Y., and J.W. Jolley, Jr. 1983. Age and growth of sailfish *Istiophorus platypterus*, using cross sections from the fourth dorsal fine spine. *In* E.D. Prince and L.M. Pulos (eds.), Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks. U.S. Dept. Commer., NOAA Tech. Rep. NMFS 8:131-135.

Hill, K.T. 1986. Age and growth of the Pacific blue marlin, *Makaira nigricans:* A comparison of growth zones in otoliths, vertebrae, and dorsal and anal fin spines. M.S. Thesis. Calif. State Univ., Stanislaus and Moss Landing Marine Laboratories, Moss Landing, Calif.:105 p.

Jolley, J.W., Jr. 1977. The biology and fishery of Atlantic sailfish *Istiophorus platypterus*, from southeast Florida. Fla. Mar. Res. Publ. 28:31 p.

Koto, T. 1963. Some considerations on the growth of marlins, using size frequencies in commercial catches. III. Attempts to estimate the growth of striped marlin, *Tetrapturus audax* (Philippi) in the western North Pacific Ocean. Rep. Nankai Reg. Fish. Res. Lab. 17:63-85.

Koto, T., and K. Kodama. 1962a. Some considerations on the growth of marlins, using size-frequencies in commercial catches. I. Attempts to estimate the growth of sailfish. Rep. Nankai Reg. Fish. Res. Lab. 15:97-108.

Koto, T., and K. Kodama. 1962b. Some considerations on the growth of marlins, using size frequencies in commercial catches. II. Attempts to estimate the growth for so called white marlin, *Marlina marlina*, (J. and H.). Rep. Nankai Reg. Fish Res. Lab. 15:109-126.

Lenarz, W.H., and E.L. Nakamura. 1974. Analysis of length and weight data on three species of billfish from the western Atlantic Ocean. *In* R.S. Shomura and F. Williams (eds.), Proceedings of the International Billfish Symposium; Pt. 2, Review and Contributed Papers. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSF-675:21-125.

Mather, F.J. III, J.M. Mason, Jr., and H.L. Clark. 1974. Migrations of white marlin and blue marlin in the western North Atlantic Ocean — tagging results since May, 1970. *In* R.S. Shomura and F. Williams (eds.), Proceedings of the International Billfish Symposium; Pt. 2, Review and Contributed Papers. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675:211-225.

Murphy, T.C., and G.T. Sakagawa. 1977. A review and evaluation of estimates of natural mortality rates of tunas. Int. Comm. Conserv. Atl. Tunas Collect. Vol. Sci. Pap. 6(1):117-123.

Nakamura, I. 1985. Billfishes of the world. FAO species catalogue, Vol. 5: 65 p. FAO Dev. Program, Rome.

Ovchinnikov, V.V., M.E. Grudtsev, and S.V. Kholodkova. 1980. Length-age composition of the tropical Atlantic swordfishes *(Xiphias gladius,* L.). Int. Comm. Conserv. Atl. Tunas Collect. Vol. Sci. Pap. 9(3):620-623.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer 30:175-192.

Powers, J.E. 1983. Some statistical characteristics of aging data and their ramifications in population analysis of oceanic pelagic fishes. *In* E.D. Prince and L.M. Pulos (eds.), Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8:19-24.

Prince, E., D. Lee, and R. Conser. 1987. Estimating age and growth of Atlantic blue marlin *(Makaira nigricans):* Progress and future work plan. Int. Comm. Conserv. Atl. Tunas Collect. Vol. Sci. Pap. 26(2):426-435.

Prince, E.D., D.W. Lee, C.A. Wilson, and J.M. Dean. 1986. Longevity and age validation of a tag-recaptured Atlantic sailfish, *Istiophorus platypterus,* using dorsal spines and otoliths. Fish. Bull., U.S. 84:493-502.

Radtke, R.L. 1983. Istiophorid otoliths: Extraction, morphology, and possible use as aging structures. *In* E.D. Prince and L.M. Pulos (eds.), Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8:123-129

Radtke, R.L., M. Collins, and J.M. Dean. 1982. Morphology of the otoliths of the Atlantic blue marlin *(Makaira nigricans),* and their possible use in age estimation. Bull. Mar. Sci. 32:498-503.

Radtke, R.L., and J.M. Dean. 1981. Morphological features of the otoliths of the sailfish, *Istiophorus platypterus,* useful in age determination. Fish. Bull., U.S. 79:360-367.

Radtke, R.L., and P.C.F. Hurley. 1983. Age estimation and growth of broadbill swordfish, *Xiphias gladius,* from the northwest Atlantic based on external features of otoliths. *In* E.D. Prince and L.M. Pulos (eds.), Proceedings of the International Workshop on Age Determination of the Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8:145-150.

Royce, W.F. 1957. Observations on the spearfishes of the central Pacific. U.S. Fish Wildl. Serv., Fish. Bull. 57:497-554.

SEFC. 1987. Report of the swordfish assessment workshop. [U.S. National Marine Fisheries Service] Southeast Fisheries Center. Int. Comm. Conserv. Atl. Tunas Collect. Vol. Sci. Pap. 26(2):339-395.

Shomura, R.S. (ed.). 1980 Summary report of the billfish stock assessment workshop Pacific resources. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-5:58 p.

Shomura, R.S., and F. Williams (eds.). 1974. Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12 August 1972; Pt. 2, Review and Contributed Papers. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675:335 p.

Shomura, R.S., and F. Williams (eds.). 1975. Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12 August 1972; Pt. 3, Species Synopses. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675:159 p.

Skillman, R.A., and M.Y.Y. Yong. 1976. Von Bertalanffy growth curves for striped marlin, *Tetrapturus audax,* and blue marlin, *Makaira nigricans,* in the central North Pacific Ocean. Fish. Bull., U.S. 74:553-566.

Wetherall, J.A., J.J. Polovina, and S. Ralston. 1987. Estimating growth and mortality in steady-state fish stocks from length-frequency data. *In* D. Pauly and G.R. Morgan (eds.), Length-based methods in fisheries research. ICLARM Conference Proceedings of the International Conference on the Theory and Application of Length-Based Methods for Stock Assessment, 11-16 February 1985, Mazzara del Vallo, Sicily, Italy:53-74.

Wild, A., and T.J. Foreman. 1980. The relationship between otolith increments and time for yellowfin and skipjack tuna marked with tetracycline. Inter-Am. Trop. Tuna Comm. Bull. 17:509-560.

Wilson, C.A., and J.M. Dean. 1983. The potential use of sagittae for estimating age of Atlantic swordfish, *Xiphias gladius. In.* E.D. Prince, and L.M. Pulos (eds.), Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8:151-156.

Yabe, H., S. Ueyanagi, S. Kikawa, and H. Watanabe. 1959. Studies on the life history of the swordfish *Xiphias gladius* Linneaus. Rep. Nankai Reg. Fish. Res. Lab. 10:106-151. (Transl. Multilingual Serv. Div., Dep. Secretary of State of Canada, 1975, 103 p.).

Yoshida, H.O. 1974. Landings of billfishes in the Hawaiian longline fishery. *In* R.S. Shomura and F. Williams (eds.), Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12 August 1972; Pt. 2, Review and Contributed Papers. U.S. Dep. Commer., NOAA Tech. Rep. NMFS-SSRF-675:297-301.

Christofer H. Boggs earned the B.S. degree (biology) in 1977 at the University of Hawaii, the M.S. degree (oceanography and limnology) in 1980, and the Ph.D. (zoology) in 1984 at the University of Wisconsin. His doctoral studies on tuna bioenergetics entailed frequent trips to Hawaii for experimental work. He is now a fishery biologist at the National Marine Fisheries Service Southwest Fisheries Center's Honolulu Laboratory, leading the Pelagic Ecosystem Task in studies of tropical tunas and their relationships with the environment.

8911

Comput Biol Med Vol 19, No 5, pp 361-366, 1989
Printed in Great Britain

0010-4825/89 $3.00 + .00
Pergamon Press plc

CARDIO—A LOTUS 1-2-3 BASED COMPUTER PROGRAM FOR RAPID CALCULATION OF CARDIAC OUTPUT FROM DYE OR THERMAL DILUTION CURVES*

R. W. BRILL† and P. G. BUSHNELL‡

†Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396, U.S.A.; and ‡John A. Burns School of Medicine, Department of Physiology, University of Hawaii, 1960 East-West Road, Honolulu, HI 96822, U.S.A.

(*Received* 15 *November* 1988; *received for publication* 22 *March* 1989)

Abstract—We have developed a menu-driven computer program (CARDIO), based on a Lotus 1-2-3 template and a series of macrocommands, that rapidly and semiautomatically calculates cardiac output from dye or thermal dilution curves. CARDIO works with any dye or thermal dilution recorder with an analog output, any analog to digital (A-to-D) conversion system, and any computer capable of running Lotus 1-2-3 version 2. No prior experience with Lotus 1-2-3 is needed to operate CARDIO, but experienced users can take full advantage of Lotus 1-2-3's graphics, data manipulation, and data retrieval capabilities.

Cardiac output   Indicator dilution   Dye dilution   Thermal dilution

INTRODUCTION

The use of dye dilution curves to measure cardiac output has become a common practice since the technique (using cardiogreen dye) was first introduced in 1929 [1]. Thermal dilution also has gained wide popularity in research and clinical settings, especially the latter, since the introduction of the Swan-Ganz† catheter [2]. Calculation of cardiac output from indicator dilution curves can be time consuming, however. If data analysis is done manually, dye dilution curves must be replotted on a semilogarithmic scale, and the downslope of the curve extrapolated to baseline because of recirculation of the dye. Thermal dilution curves must be similarly treated [3].

Analog computers have been developed for both dye and thermal dilution systems, but these instruments are expensive and have a single purpose [4]. Techniques have been published for more rapid or automatic calculation of cardiac output from dye dilution curves [5-7], but all require either specialized equipment or manual measurement of curve heights. The computer program (CARDIO) described here is based on a Lotus 1-2-3 template and a series of Lotus 1-2-3 macrocommands. It is more rapid and accurate and less subject to human error than are previously published techniques.

THEORY OF OPERATION

CARDIO uses a data set consisting of elapsed time and the corresponding voltage output from the dye or thermal dilution recording instrument. Once imported into the Lotus 1-2-3 template, the voltage data are converted to natural logarithms, and a linear regression is performed on the downslope of the indicator curve. This is equivalent to

---

* A copy of CARDIO and a sample dye dilution curve data set will be provided either on a 5 1/4 or 3 1/2 inch DS/DD floppy disk. Instructions for program execution and modification also will be included.

† Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

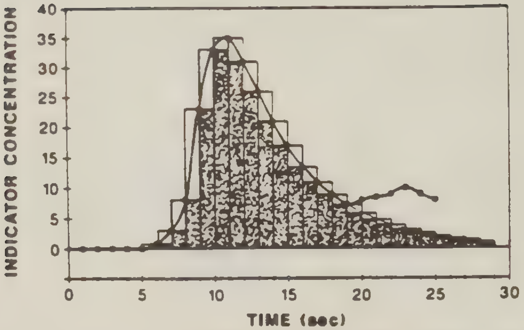


Fig. 1. Graphical representation of summation procedure used to estimate areas under indicator dilution curves. Shaded rectangles are summed to calculate minimum curve areas. Maximum area is calculated from the shaded plus clear rectangles. Data are from [5].

fitting an exponential decay curve

$$C = C_0 \cdot e^{-k \cdot t}; \tag{1}$$

where C = indicator concentration, C_0 = indicator concentration at time zero, k = rate constant of indicator decay, t = elapsed time, and e = base of the natural logarithm [8]. The downslope of the indicator curve is extrapolated, based on this regression, until the curve falls below a user-selectable value (baseline).

Maximum (Area_{max}) and minimum (Area_{min}) areas under the curve are calculated by numerical integration (trapezoidal rule) over $n - 1$ time intervals:

$$\text{Area}_{\text{max}} = \sum_{i=1}^{n-1} (V_{i+1})(t_{i+1} - t_i) \tag{2}$$

and

$$\text{Area}_{\text{min}} = \sum_{i=1}^{n-1} (V_i)(t_{i+1} - t_i); \tag{3}$$

where V_i = voltage at time t_i, V_{i+1} and t_{i+1} = the next recorded time–voltage data pair, and n = the total number of time–voltage data pairs. The area under the curve (Area_{avg}) used for cardiac output calculations is taken as the average of Area_{max} and Area_{min}. This technique is shown graphically in Fig. 1.

Cardiac output (Q) is calculated using the amount of indicator injected (I) and a calibration factor (F) that converts recorder voltage output to dye concentration.

$$Q = \frac{I \cdot F}{\text{Area}_{\text{avg}}}. \tag{4}$$

METHOD OF OPERATION

Any A-to-D system is usable, and satisfactory, single-channel A-to-D systems are currently available for less than US$200. Only a simple program to create and record an ASCII data file of the recorder's voltage output and elapsed time is needed. Figure 2 is a BASIC language program that may be used as a guide. The only requirements are that the file name have the extension ".PRN" required by Lotus 1–2–3 for importing data files, that the first line be a string, and that the data be separated by commas or blank spaces.

Our BASIC program example stores a unique identifier string at the beginning of each data file, which is the same as the file name. However, any other identifier is acceptable. Used as a title for all graphs produced by CARDIO, this identifier is also printed with the cardiac output data summary (Fig. 3). Our program example stores the data in memory before writing it to disk and contains a loop (line 110) that slows data collection to avoid computer memory or buffer overflow. The delay loop may be modified or eliminated to suit data collection needs. Data may also be written directly to disk, but this may make

```
10 DIM V(600), ET(600)               'dimension voltage and elapsed time
20 KEY(1) ON                         'set up function key F1
30 INPUT "ENTER FILE NAME ", FILE$   'user prompted for the file name
40 FILE$ = FILE$ + ".PRN"            'add file name extension required by
                                      Lotus 1-2-3 for importing data files
50 START! = TIMER                    'read internal real time clock and
                                      define time zero
60 ON KEY(1) GOTO 130                'use function key F1 to halt data
                                      collection and write data to disk
70 ETIME! = TIMER                    'read internal real time clock
80 I=I+1                             'counter for writing stored data to
                                      disk
90 'Program lines to read analog to
   digital converter placed here.

100 ET = ETIME! - START!             'calculate elapsed time
110 FOR Z = 1 TO 500: NEXT I         'slow operation of data collection loop
120 GOTO 70                          'repeat data collection loop
130 OPEN FILE$ FOR OUTPUT AS #1      'set up disk file name
140 WRITE #1, FILE$                  'store file name (string) beginning of·
                                      the data file
150 FOR J = 1 TO I                   'repeat until all voltage-elapsed time
                                      pairs have been written to disk
160 WRITE #1, J, V(J), ET(J)         'write voltage (V) and elapsed time
                                     (ET) data to disk
170 NEXT J: CLOSE                    'when completed, close the file
```

Fig. 2. BASIC language program for digitizing indicator dilution curves and storing the data on disk. The program will produce a data set suitable for use with CARDIO.

```
************************************************
*           CARDIAC OUTPUT CALCULATIONS        *
*  .........     A:SJ1230-8.PRN    .........   *
*                                              *
*  DYE CONCENTRATION=         1.96 mg/ml       *
*  AMOUNT INJECTED=           0.1 ml           *
*  CALIBRATION FACTOR=       46.2 v/mg/ml      *
*                                              *
*  CURVE AREA=                4.700 v-s        *
*  REGRESS COEFF=             0.998            *
*                                              *
*  ANIMAL WEIGHT=             1.411 kg         *
*  - - - - -- - -- - - - - - - - - -- - - -    *
*  CARDIAC OUTPUT=          115.7ml/min        *
*                            81.9 ml/min/kg    *
************************************************
```

Fig. 3. Example of data summary produced by CARDIO. Curve area and regression coefficient (based on indicator dilution curve's downslope) are automatically produced by the program. The user then enters the dye concentration, amount of dye injected, and a calibration factor for the dye measurement instrument; whole animal and weight-specific cardiac output are then calculated by the program.

data collection unacceptably slow in some systems. Note that in line 160 a sequence number also is stored along with voltage and elapsed time. Sequence numbers are required because they are used as a means of identifying the curve's baseline in CARDIO.

After the indicator dilution curve is stored, Lotus 1-2-3 is loaded, and the template "CARDIO.WK1" retrieved. Instructions for running CARDIO and an operations menu are automatically presented. The items on the operations menu are selected and executed, as are other Lotus 1-2-3 commands, either by pointing or by typing their first letter. The indicator dilution data file must first be "imported" into the template by executing "Import". This macrocommand retrieves the data file from disk and automatically creates and graphs a semilogarithmic plot of the elapsed time–voltage data, as shown in Fig. 4a. From this plot, the operator selects the voltage to be used for the baseline (or steady state portion) of the curve and the data points on the downward slope to be used for the semilogarithmic linear regression and eventual extrapolation. Next, a series of macrocommands are executed that extrapolate the downslope of the curve to the end of the collected elapsed time–

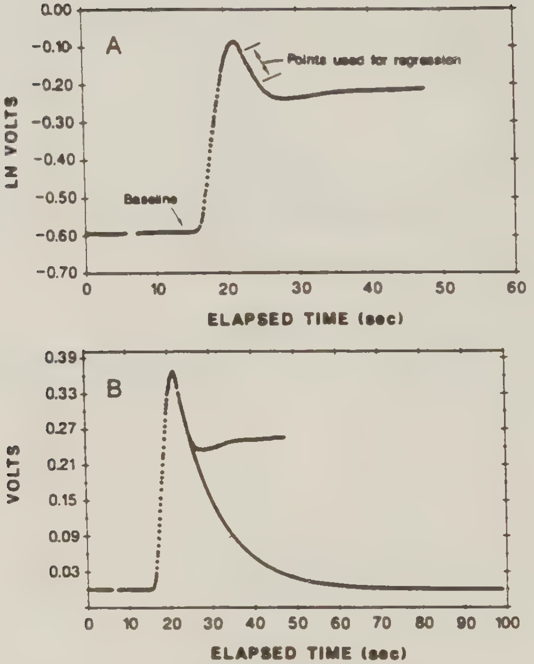


Fig. 4. An example of the semilogarithmic plot (a) and the extrapolated and extended curve (b) produced by CARDIO. The data are from a dye dilution curve from a skipjack tuna (*Katsuwonus pelamis*). Data were recorded approximately every 0.1 s. The linear portion of the curve's downslope, to be used for curve extrapolation, can be easily recognized. The data for these plots were produced by CARDIO and then replotted using Sigmaplot, a commercial plotting program, and a Hewlett–Packard 7475A pen plotter.

voltage data. If the extrapolated curve has reached or gone below the baseline at this time, the area under the curve is calculated, and the operator presented with a summary form (Fig. 3) in which values for dye concentration, amount of dye injected, calibration factor for recording instrument, and animal weight are entered. Once these data are entered, a final macrocommand is executed, and cardiac output automatically calculated.

The program also has two additional capabilities. One, if the curve does not reach baseline by the end of the collected data, the curve will automatically be extended until it falls below baseline. The time increments used for curve extension can be set by the operator. A curve extended in this manner, using 1 s increments, is shown in Fig. 4b. Two, a second macrocommand is available to correct for a linearly drifting baseline. The operator selects a portion of the baseline to be used for the linear regression, and the program automatically corrects the entire curve by subtracting or adding a value proportional to the elapsed time.

PROGRAM PERFORMANCE AND TESTING

To verify CARDIO's performance, we calculated the cardiac output from a digitized dye dilution curve published by Lin [5] and shown in Fig. 1. Using the same points on the downslope to perform the regression for curve extrapolation, CARDIO calculated a curve area of 268.3 unit seconds (indicator concentration was given in arbitrary units) and a cardiac output of 1.490 l/min (for a 19.6 kg dog). Lin [5] calculated a curve area of 263.2 unit seconds and cardiac output of 1.519 l/min. The small differences are most likely the result of Lin's [5] apparently extrapolating the curve's downslope until it fell below 0.9

Table 1. Effect of baseline value on execution* time, mean calculated curve area, and final size of the worksheet for the dye dilution curve in Figs 4 and 5

Baseline	Execution time (s)	Mean curve area (volt·s)	Final size of worksheet (lines)
1×10^{-3}	77	4.628	454
1×10^{-4}	88	4.692	476
1×10^{-5}	101	4.700	498
1×10^{-6}	112	4.701	421
1×10^{-7}	125	4.702	643
1×10^{-10}	164	4.702	609
1×10^{-13}	205	4.702	675

* Time required to extrapolate and extend curve to below baseline and calculate area under the curve.

Table 2. Effect of sampling rate on mean calculated curve area. Data are from dye dilution curve shown in Fig. 4. The original sampling interval was approximately 0.1 s

Approximate sampling interval (s)	Mean curve area (volt·s)
1.0	5.178
0.5	4.701
0.2	4.676
0.1	4.702

units. CARDIO extrapolated the downslope until the curve fell below 0.0001 units and, therefore, produced a larger estimate of curve area and a smaller estimate of cardiac output. The difference in cardiac output estimates is <2%.

Equation (1) shows that systems exhibiting exponential decay will only approach zero concentrations as elapsed time approaches infinity. An arbitrary baseline value, insignificantly different from zero, must be chosen as a cutoff point to terminate curve extrapolation. This baseline value may be adjusted for the range of the dye or thermal recorder's output (e.g. volts or millivolts). The value chosen will affect the accuracy of the curve area estimate, the final size of the worksheet (and the amount of computer memory required), and the execution time of the program. Using the data shown in Fig. 4, CARDIO was tested with various baseline values. The results (Table 1) indicate that curve area estimates are asymptotic and that choosing too small a baseline value will significantly increase execution time and the amount of computer memory required.

The effect of sampling rate (i.e. rate of A-to-D conversion of the indicator dilution curve) also was tested using the data from the curve in Fig. 4. Decreased data sampling rates were simulated by repeatedly removing every other data point from the original data set. Results are shown in Table 2. Higher sampling rates necessarily result in better estimates of curve area, but sampling rates are constrained by the computer memory available for use with CARDIO. CARDIO is currently designed to accept up to 600 elapsed time–voltage data pairs. This requires an available memory of 155 Kbytes after Lotus 1–2–3 is loaded. In other words, a minimum total available memory of approximately 412 Kbytes is needed. Template size may be easily increased if a larger number (i.e. >600) of elapsed time–voltage data pairs must be accommodated. The amount of data that can be handled is limited only by the amount of total (base plus expanded) computer memory and the maximum size of Lotus 1–2–3 worksheets (8,192 lines).

ADVANTAGES OF CARDIO

Our program has distinct advantages over other techniques currently available. First, it requires only hardware and software (an IBM personal computer or equivalent, Lotus 1–2–3 version 2, any single or multichannel analog to digital (A-to-D) conversion system, and any dye or thermal dilution recording system with an analog output)—all of which are already available in many laboratories. Second, because no manual data manipulation is performed, high rates of data collection can be handled, and inaccuracies due to manual measurement of curve heights or areas can be avoided. Nevertheless, the user is able to select the data points to be used for extrapolation of the downslope of the curve from a semilogarithmic curve presented on the computer screen and to edit the data as required. Third, use of the program can be easily learned because it is totally menu driven and requires no familiarity with Lotus 1–2–3 itself. Experienced Lotus 1–2–3 users, however, can take full advantage of this package's graphics, data manipulation, and data storage and retrieval capabilities. Fourth, because of the flexibility of Lotus 1–2–3, the template can be easily customized for use with either dye or thermal dilution curves, to fit available computer memory and to optimize execution time and the required accuracy. Fifth, CARDIO allows the rapid calculation of cardiac output. Using an IBM AT computer, we found that the average time to calculate cardiac output from dye dilution curves that include approximately 400–600 data points (dye dilution measurements recorded at approximately 10 times per second) was <4 min.

SUMMARY

The estimation of cardiac output from indicator dilution curves can be time consuming if done manually, because of the replotting required to determine the curve's downslope in the face of indicator recirculation and the manual measurement of area under the indicator concentration curve. Although analog computers are available to automate the process, they are expensive and have a single purpose. We have developed a program, based on a series of Lotus 1–2–3 macrocommands, that automatically extrapolates the curve's downslope and then calculates area under the curve and cardiac output. Our program has the advantages of working with any dye or thermal dilution recorder with an analog output, any A-to-D conversion system, and any computer capable of running Lotus 1–2–3. Our program, therefore, takes advantage of equipment already common in many laboratories to make a semiautomatic cardiac output measurement system. Because of the flexibility of Lotus 1–2–3, the program may be easily customized to fit available computer memory, meet the required degree of accuracy, and work with thermal or dye dilution systems.

REFERENCES

1. J. M. Kinsman, J. W. Moore and W. F. Hamilton, Studies on the circulation. I. Injection method: physical and mathematical considerations, *Am. J. physiol.* **89**, 322–339 (1929).
2. K. C. Ehlers, K. C. Mylrea, C. K. Waterson and J. M. Calkins, Cardiac output measurements. A review of current techniques and research, *Ann. Biomed. Engng.* **14**, 219–239 (1986).
3. D. J. Warren and J. G. G. Ledingham, Cardiac output in the conscious rabbit: an analysis of the thermodilution technique, *J. appl. Physiol.* **36**, 246–251 (1974).
4. T. G. Coleman and F. J. Criddle Jr, Computerized analysis of indicator-dilution curves, *J. appl. Physiol.* **28**, 358–360 (1970).
5. Y. C. Lin, A programmable calculator program for rapid logarithmic extrapolation, and calculation of mean transit time from an indicator-dilution curve, *Comput. Program. Biomed.* **9**, 135–140 (1979).
6. P. M. Olley, B. S. L. Kidd and S. Zelin, Cardiac output: rapid estimation form indicator dilution curves using a new nomogram, *Can. J. Physiol. Pharmacol.* **48**, 147–149 (1970).
7. J. C. P. Williams, T. P. B. O'Donovan and E. H. Wood, A method for the calculation of areas under indicator-dilution curves, *J. appl. Physiol.* **21**, 695–699 (1966).
8. D. S. Riggs, *The Mathematical Approach to Physiological Problems*, p. 445. MIT Press, Cambridge, MA (1963).

About the Author—RICHARD W. BRILL received a B.A. in biology from Lafayette College in 1970, a Masters in biology from Northeastern University in 1974, and a Ph.D. in biomedical sciences from the Physiology Department, John A. Burns School of Medicine, University of Hawaii in 1979. Following a one-year postdoctoral fellowship at the University of British Columbia, Dr Brill returned to Hawaii as Director of the Pacific Gamefish Research Foundation. He joined the staff of the National Marine Fisheries Service (Southwest Fisheries Center Honolulu Laboratory) in 1983 and is currently a member of the Pelagic Ecosystem Program.

About the Author—PETER G. BUSHNELL received a B.S. in biology from the University of Maryland in 1976, a Masters in marine biology from the University of Miami in 1982, and a Ph.D. in biomedical sciences from the Physiology Department, John A. Burns School of Medicine, University of Hawaii in 1989. Dr Bushnell is currently a postdoctoral fellow in the Department of Zoology, University of British Columbia.

8912

MARINE MAMMAL SCIENCE, 5(2):193–195 (April 1989)
© 1989 by the Society for Marine Mammalogy

A PORPOISE, *AUSTRALOPHOCAENA DIOPTRICA*, PREVIOUSLY IDENTIFIED AS *PHOCOENA SPINIPINNIS*, FROM HEARD ISLAND

Guiler, Burton and Gales (1987) reported a cranium (Tasmanian Museum No. A1411) they identified as belonging to Burmeister's porpoise, *Phocoena spinipinnis* Burmeister, 1865 from Heard Island (53°S 73°30′E). They noted that *P. spinipinnis* was previously known only from the cold-temperate coastal waters of South America and claimed that this cranium was evidence that the species has a much wider distribution than previously known. We have examined the photographs and details of their specimen and re-identify it here as *Australophocaena dioptrica* (Lahille, 1912) (family Phocoenidae).

Barnes (1985) listed several features that distinguish the skulls of species within the subfamily Phocoenoidinae (including *A. dioptrica*) from those species within the Phocoeninae (including *Phocoena* spp.). Features that distinguish *A. dioptrica* from *P. spinipinnis*, clearly visible in the published photographs of the cranium from Heard Island, include: a relatively small, oval-shaped temporal fossa; an elevated, high-vaulted braincase that slopes abruptly onto the narial region; relatively large, high and convex premaxillary bosses; dorso-ventrally expanded zygomatic process of the squamosal; short and anteroposteriorly expanded postorbital process of the frontals; and maxillae extending nearly to the dorsal margin of the supraoccipital on the top of the skull. In all these features, the Heard Island specimen conforms with those of *A. dioptrica*. Crania of *A. dioptrica* have been illustrated by Hamilton (1941), Norris and McFarland (1958), Brownell (1975), Fordyce *et al.* (1984), and Barnes (1985). Crania of *P. spinipinnis* have been illustrated by Norris and McFarland (1958) and Brownell and Praderi (1984).

While *Phocoena spinipinnis* and *Australophocaena dioptrica* overlap in adult skull length, the Heard Island specimen is larger than any known specimen of *P. spinipinnis*. The condylobasal length (CBL) of this cranium is 303 mm; CBL in 10 specimens of *P. spinipinnis* examined by Brownell and Praderi (1984) was 224 to 290 mm. The same measurement for 46 adult skulls of *A. dioptrica* ranged from 279 to 324 mm (unpublished data, WFP).

Guiler *et al.* (1987) based their identification of the newly discovered specimen on a comparison of the photographs of phocoenid skulls presented by Norris and McFarland (1958). They noted that although the cranium from Heard Island was larger than the specimen of *P. spinipinnis* shown by Norris and McFarland (1958), "the ratio of rostral width : rostral length (0.513) is similar to that found by those two authors (0.517) as is the ratio of skull length : skull width (0.55 compared to 0.560). These ratios are different from those found for *P. sinus* (0.630 and 0.637 respectively) and for *P. phocaena* [*sic*] (0.470 and 0.537). The rostral proportions for *A. dioptrica* are 0.737."

The ratio of the width to length of the rostrum of the cranium from Heard Island is given by Guiler *et al.* (1987) as 0.513, but, based on the measurements given in their table 1, it is actually 0.506 (82 divided by 162). Moreover, the rostral length of the Heard Island specimen (162 mm) given in this table must be incorrect. If the zygomatic width and the maximum width are both 169 mm, then it can be seen in figure 2 of Guiler *et al.* (1987) that the rostral length is only about 75% of the maximum width, or approximately 127 mm. This new value for the rostral length of the cranium would give a width to length ratio of 0.646. This ratio would be greater if the rostral length were less. To obtain a rostral length as great as 162 mm, the measurement would necessarily have been made from the tip of the rostrum to the external nares; and we believe that the rostral length measurement must have been made in this way. The correct ratio of approximately 0.646, therefore, is closer to that of *A. dioptrica* than *P. spinipinnis*.

The ratio of skull width to the total length of the cranium is 0.558 (not 0.550 as given by Guiler *et al.*). The same ratio in the specimens reported by Norris and McFarland (1958) for *P. spinipinnis* is 0.615 (168 divided by 273) and 0.583 for *A. dioptrica*. Again the ratio of the specimen from Heard Island is closer to that of *A. dioptrica* than to that of *P. spinipinnis*.

We are not able to comment on the rostral alveolar count (14 left and 13 right) given for the Heard Island specimen, except to say that a few extra teeth in each tooth row would yield a number corresponding to the lower end of the range for *A. dioptrica* (16–25 in ten specimens recently examined by WFP). The posterior-most teeth in this species are in a shallow aveolar groove and are easily lost and their numbers very difficult to determine from dry specimens.

Specimens of *A. dioptrica* have been previously reported from Uruguay, Argentina, southern Chile, the Falkland Islands (Malvinas), South Georgia, the Auckland Islands and Macquarie Island (Brownell 1974, Baker 1977, Goodall and Cameron 1979, Fordyce *et al.* 1984). At-sea sightings of the species are known from around New Zealand and Kerguelen Islands (Frost and Best 1976, Fordyce *et al.* 1984). Thus, the specimen reported by Guiler *et al.* (1987), which we identify as *A. dioptrica*, extends the known distribution of the species, which is in the cool-temperate waters of the southern ocean in subarctic latitudes. It will be interesting if future records fill in this scattered distribution record.

Phocoena spinipinnis remains a species of southern South America (coastal waters of southern Brazil—Pinedo, in press; Uruguay, Argentina, Chile and Peru—Brownell and Praderi 1984). The species is not even known from the Falkland Islands, where two other dolphins inhabiting the South American mainland coastal waters (*Cephalorhynchus commersonii* and *Lagenorhynchus australis*) are known (Brownell 1974).

We thank L. G. Barnes and K. Ralls for useful comments on this manuscript. E. R. Guiler kindly provided photographs of his Heard Island specimen. The unpublished cranial data for *A. dioptrica* were collected as part of a study in progress by WFP, R. N. P. Goodall and M. Cozzuol.

LITERATURE CITED

BAKER, A. N. 1977. Spectacled porpoise, *Phocoena dioptrica,* new to the subantarctic Pacific Ocean. New Zealand Journal of Marine and Freshwater Research 11:401–406.

BARNES, L. G. 1985. Evolution, taxonomy and antitropical distributions of the porpoises (Phocoenidae, Mammalia). Marine Mammal Science 1:149–165.

BROWNELL, R. L., JR. 1974. Small odontocetes of the Antarctic. Pages 13–19 *in* V. C. Bushnell, ed. Antarctic mammals, Folio 18, Antarctic Map Folio Series, American Geographical Society, New York.

BROWNELL, R. L., JR. 1975. *Phocoena dioptrica.* Mammalian Species 66:1–3.

BROWNELL, R. L., JR., AND R. PRADERI. 1984. *Phocoena spinipinnis.* Mammalian Species 217:1–4.

FORDYCE, R. E., R. H. MATLIN AND J. M. DIXON. 1984. Second record of spectacled porpoise from subantarctic southwest Pacific. Scientific Reports of the Whales Research Institute 35:159–164.

FROST, P. G. M., AND P. B. BEST. 1976. Design and application of a coded format for recording observations of cetaceans at sea. South African Journal Antarctic Research 6:9–14.

GOODALL, R. N. P., AND I. S. CAMERON. 1979. *Phocoena dioptrica,* una nueva especie para aguas chilenas. Revista del Museo Argentino de Ciencias Naturales, "Bernardino Rivadavia." Zoología 12(11):143–152.

GUILER, E. R., H. R. BURTON AND N. J. GALES. 1987. On three odontocete skulls from Heard Island. Scientific Reports of the Whales Research Institute 38:117–124.

HAMILTON, J. E. 1941. A rare porpoise of the South Atlantic, *Phocoena dioptrica* (Lahille, 1912). Discovery Reports 21:222–234 + 2 plates.

NORRIS, K. S., AND W. N. MCFARLAND. 1958. A new harbor porpoise of the genus *Phocoena* from the Gulf of California. Journal of Mammalogy 39:22–39.

PINEDO, M. C. In press. Primeiro registro de *Phocoena spinipinnis* (Cetacea, Phocoenidae) para o litoral do Rio Grande do Sul, Brasil, com medidas osteológicas e análise do conteúdo estomacal. Revista Atlantica.

ROBERT L. BROWNELL, JR., U.S. Fish and Wildlife Service, P.O. Box 70, San Simeon, California 93428; JOHN E. HEYNING, Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, California 90007; WILLIAM F. PERRIN, Southwest Fisheries Center, P.O. Box 271, La Jolla, California 92038.
Received June 15, 1988. Accepted November 29, 1988.

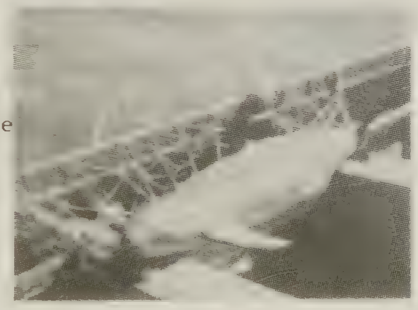
8913

The Plight of the 'Forgotten' Whales

It's mainly smaller cetaceans that are now in peril

by Robert L. Brownell, Jr., Katherine Ralls, and William F. Perrin

The "Save the Whales" movement, the most successful wildlife crusade in history, has greatly influenced government policies in a number of countries, including the United States. Thanks in large part to the movement's dedicated members, the fight to save the great whales has been largely won. Yet all but ignored in this victory has been the plight of smaller cetaceans, which continues to worsen.



This vaquita drowned in gillnets set to study the fish totoaba in the upper Gulf of California.

The pivotal year for the great whales was 1970, when nine of the 12 species were listed as endangered under the U.S. Endangered Species Act (ESA, box, pp. 12–13). At that time they met the ESA's definition of an endangered species (Table 1). They were overexploited by commercial whalers and inadequately protected by laws and regulations. These are now two of the five criteria that must be considered when species are listed or taken off the list under the ESA (Table 2). Although the ESA list still includes all the great whales that were originally on it, the major concerns that prompted their inclusion are no longer relevant.

Some of the great whales have been completely protected by the International Whaling Commission (IWC) for many years. Now all of them are protected under the moratorium on commercial whaling implemented by the IWC in 1986. In that year, 7,200 great whales were killed,* compared to more than 55,000 in 1966. Fewer than 700 were killed in 1988, all under the research or subsistence provisions of the IWC moratorium which expires in 1991.

In marked contrast to the improving prospects for the great whales, the status of many smaller cetaceans has continued to deteriorate over the last two decades. Some species and local populations of dolphins, porpoises, and small whales are in greater danger of extinction than any of the great whales, except possibly the northern right whale, *Eubalaena glacialis*. For example, the population of the baiji, or Chinese River dolphin, *Lipotes vexillifer*, is believed to be down to only about 300 individuals. Each year hundreds of thousands of other small cetaceans are killed incidentally in various fisheries around the world. However, the situation of most of these smaller cetaceans has received relatively little public attention—indeed, they are almost forgotten species—and they receive almost no legal protection, except for the regulation of the U.S. tuna/dolphin fishery and the kill of Dall's porpoise, *Phocoenoides dalli*, in Japanese salmon gillnets. Only one small cetacean, the vaquita, or Gulf of California harbor porpoise, *Phocoena sinus*, is currently on the U.S. Endangered Species List, and it wasn't even listed until 1985.

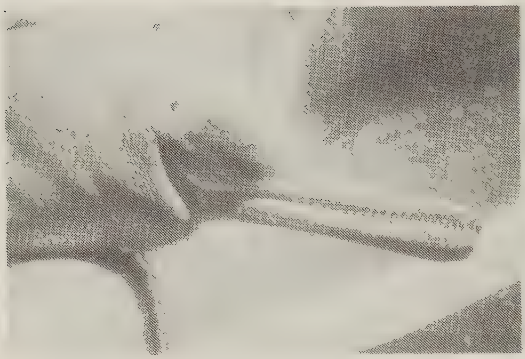
But before we look at the small cetaceans in detail, we will briefly review the status of their larger relatives.

The Condition of the Great Whales

The northern right whales and southern right whales, *Eubalaena australis*, earned their name because they were were easy to capture and floated when dead—they were the "right" whales to hunt. They were pursued from early times in the coastal waters of temperate latitudes in both hemispheres until all populations were reduced to extremely low numbers. For about 50 years

---

*Most of these whales were taken by Japan, the Soviet Union, and Norway. These countries had lodged formal objections to the moratorium and so were allowed by the rules of the IWC to set their own quotas and continue whaling. Norway and the Soviet Union ceased commercial whaling in 1987, and Japan in 1988.



A female Indus river dolphin. Only 500 of this species survive. (Photo by Earl S. Herald)

Feeding goldfish to a pair of Irrawaddy dolphins in Jakarta. (Photo by Helene Marsh)

now, they have received almost complete protection in most parts of their ranges. Some populations in the southern hemisphere are beginning to increase. We believe there are about 3,000 right whales in these southern hemisphere stocks. However, there is still no evidence of population growth in the northern hemisphere stocks, which may number less than 500. Reduced along with some of the stocks of the bowhead whale, *Balaena mysticetus*, to the lowest levels of any whale populations, it may take decades before these stocks show signs of increase.

Historically, bowheads were found in virtually all Arctic waters. The commercial fishery began during the 17th century and lasted until the early part of this century. Commercial exploitation ended when the value of the bowhead's two main products—baleen and whale oil—was reduced drastically by the development of spring steel and petroleum products. Since the 1920s, the bowhead has been hunted only from about two dozen coastal villages in the United States and the Soviet eastern Arctic, and in the last decade, only by the Alaskan Inuit. The largest remaining stock of this species, about 7,800 whales, ranges throughout the Bering, Chukchi, and Beaufort Seas (article pp. 54–62).

The gray whale, *Eschrichtius robustus*, originally roamed the northern hemisphere along the coasts of both the Atlantic and Pacific Oceans. It became extinct in the North Atlantic in the 1700s, possibly because of overexploitation by Basque and American whalers, and was hunted to low numbers on both sides of the North Pacific in the last century. The eastern, or California, population has been protected by the IWC since 1946. A regulated catch of about 180 is taken each year off the Chukotka Peninsula of the Soviet Union for subsistence use. Since it was protected, the population has increased to more than 20,000 animals, which is thought to be within the range of its prewhaling level.

Protecting the Humpbacks

Humpback whales, *Megaptera novaeangliae*, are found worldwide. Their coastal migrations made them extremely vulnerable to overexploitation, and they were greatly depleted throughout the world by both land station and pelagic whaling operations. Since 1966, the IWC has protected humpbacks from commercial whaling throughout the world. A subsistence fishery off Greenland ended in 1987. Limited subsistence hunting is allowed in the Caribbean (*Oceanus*, Vol. 30, No. 4, pp. 89–93). The present world population is estimated to be more than 10,000 whales.

The blue and fin whales, *Balaenoptera musculus* and *B. physalus*, were not exploited until the invention of fast steam ships and the grenade harpoon in the second half of the 19th century. Nevertheless, the blue whale was severely depleted in the southern hemisphere to less than 10 percent of its original estimated population. The last blue whales taken in the southern hemisphere were caught in 1967. Although they have been totally protected for more than 20 years by the IWC, there has been no detectable increase in numbers over that period. In the northern hemisphere, however, groups of blue whales are commonly seen in the waters off Sri Lanka, California, and Baja California, and in the Gulf of St. Lawrence. The worldwide population is currently less than 10,000 individuals.

After the decline of the blue whales, the fin whale constituted the major portion of the world's catch of whales. More than 100,000 fin whales were taken during the 1960s alone. As a result, some populations were depleted, especially those in the southern hemisphere. The remaining southern hemisphere fin whales have been protected by the IWC since the early 1970s,

---

Robert L. Brownell, Jr., Katherine Ralls, and William F. Perrin are research scientists with the U.S. Fish and Wildlife Service, the Smithsonian Institution, and NOAA Fisheries, respectively. (All photos in this article are by Brownell unless otherwise noted.)

but catches continued in the North Pacific until 1975, and a small research catch is still allowed under special permit each year by Iceland in its waters (article, pp. 29-36). Last year Iceland caught 68 fin whales. The present worldwide population estimate is imprecise, but is on the order of 150,000 animals.

During the 1960s, following the fin whale's decline, sei whales, *B. borealis*, were heavily exploited in the southern hemisphere. These large catches—22,205 whales landed in 1965 alone—greatly reduced this last species of large whale in the area. Smaller catches of sei whales occurred in the North Pacific and North Atlantic throughout most of the 20th century. The IWC has protected the North Pacific stocks since 1976, and had protected all North Atlantic stocks prior to the 1986 commercial whaling moratorium. A rough worldwide estimate is at least 50,000 whales.

Bryde's whale, *B. edeni*, usually lives in tropical and subtropical waters, but sometimes visits cooler areas. This species has not been of major importance in commercial pelagic whaling, but has been taken in the coastal waters of the western Pacific, and off Brazil, Peru, and South Africa. Catch records are confusing because of the difficulty of distinguishing Bryde's whale from sei whales.

The minke whale, *B. acutorostrata*, is the smallest of the great whales. Although various coastal countries in the northern hemisphere have captured minke whales for much of the last 50 years, commercial exploitation by pelagic whaling operations in the Antarctic did not begin until the early 1970s, and ceased after Japan's 1986/87 season. The southern hemisphere populations are currently estimated to be more than a half million individuals. Japan began some low-level research catches of about 300 whales a year in the Antarctic in 1988. The only minke whales taken in the northern hemisphere during 1988 were 30 for research by Norway, and about 110 off Greenland for subsistence.

Little is known about the pygmy right whale, *Caperea marginata*, that occurs in temperate waters of the southern hemisphere, since few specimens have ever been examined by scientists and it has never been exploited commercially. Even sightings at sea are rare.

Sperm whales (usually known as *Physeter catodon*, but also referred to as *P. macrocephalus*) are found in all the oceans, from the equator to the polar seas. They have been the subject of two major phases of whaling: "old" whaling, mainly from the mid-18th to mid-19th centuries; and "modern" whaling, particularly between 1946 and 1980. Catches were taken by pelagic and coastal operations. During the latter phase most catches were taken in the North Pacific. In 1966, the world catch was more than 27,000 whales. The fishery concentrated on large males in many areas, and much of the recent concern of scientists has centered on possible effects of this selective removal on reproductive rates. All commercial whaling on this species has now stopped, but subsistence or traditional whaling continues in some areas, such as Indonesia and the Azores. Although some local stocks are still considered depleted by the IWC, other stocks contain tens of thousands of whales.

Status of Some Small Cetaceans

While long-term protection of the great whales has allowed populations to begin to recover, or at least stabilize, the situation for many small cetaceans is bleak. Overhunting and destruction of habitats have brought various populations to dangerously low levels, yet only one species is listed as endangered under the ESA.

The vaquita, or Gulf of California harbor porpoise, an endemic species known only from the upper third or so of the Gulf of California, Mexico, was listed in 1985 by the National Marine Fisheries Service, an arm of the National Oceanic and Atmospheric Administration (NOAA). This species was first described in 1958 from specimens that were probably captured incidentally in a gillnet fishery for totoaba, a large fish. The Mexican government closed the totoaba fishery in 1975 because the fish population had declined dramatically. Closure of this fishery

Table 1. Terms to describe the status of cetaceans.

U.S. List of Threatened and Endangered Species

Endangered: Any species which is in danger of extinction throughout all or a significant portion of its range.

Threatened: Any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range.

IUCN (International Union for the Conservation of Nature and Natural Resources) Red List

Endangered: In danger of extinction, survival unlikely if causal factors continue operating. Includes taxa whose members have been reduced to a critical level or whose habitats have been so drastically reduced that they are deemed to be in immediate danger of extinction.

Vulnerable: Taxa believed likely to move into the endangered category in the near future if the causal factors continue operating. Included are taxa of which most or all of the populations are decreasing because of overexploitation, extensive destruction of habitat, or other environmental disturbance; taxa with populations that have been seriously depleted and whose ultimate security has not been assured and taxa with populations that are still abundant but are under threat from severe adverse factors throughout their range.

Insufficiently known: Taxa that are suspected but not definitely known to belong to any of the above categories, because of lack of information.

Dall's porpoise, found only in the North Pacific.

The baiji, probably the world's most endangered cetacean. (Photo by Clifford H. Pope)

reduced the incidental mortality of porpoises, but other fishery operations continued to catch some vaquitas. The Mexican government has unfortunately allowed research catches of totoaba since 1985, and recently many vaquitas have been taken incidental to these fishing operations. While little is known about the biology and present population levels of this porpoise, it must be considered endangered.

Several species of river dolphins deserve special attention. Although none are listed by the ESA, two species are listed as "endangered" on the Red List of Threatened Animals published by the International Union for the Conservation of Nature and Natural Resources (IUCN), located in Gland, Switzerland.

The baiji is probably the most endangered of all cetaceans. Only a few hundred remain in the Yangtze River and their numbers appear to be decreasing. The baiji no longer occurs in many areas where it was found 70 years ago, when it was first scientifically described. A major cause of mortality is entanglement in bottom longlines equipped with fishhooks every few centimeters. This "rolling hook" fishing gear happens to be laid in regions with the highest baiji densities. Although China has declared the species a "Protected Animal of the First Order," significant numbers continue to be killed incidentally by such human activities as fisheries, boat traffic, and explosions from construction work. The Chinese have proposed two seminatural reserves for the baiji; the consensus of scientists attending a recent workshop in China on river dolphins was that work should begin on both reserves as quickly as possible.

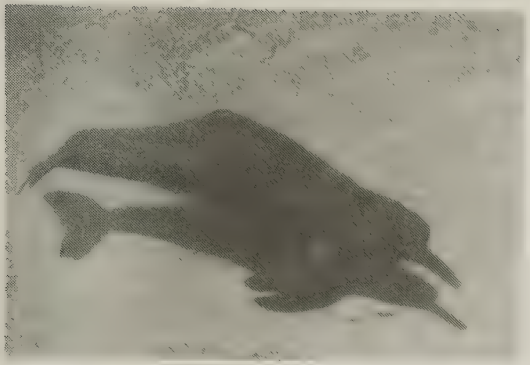
The Indus river dolphin, *Platanista minor*, is also in danger, with a total world population of about 500 individuals. More than 400 are protected in a reserve, but the remaining animals are divided into four isolated and unprotected populations in the Punjab of Pakistan. Many populations in the Punjab have already disappeared, and surveys indicate that the remaining populations outside the reserve are declining rapidly.

Although not as critically endangered as the Chinese and Indus river dolphins, other species of river dolphins are of concern. Populations of the Ganges river dolphin, *Platanista gangetica*, seem to be declining due to human activities in India, Bangladesh, and Nepal, and rapid development in the Amazon River basin is resulting in the loss of essential habitat for the boto, or Amazon river dolphin, *Inia geoffrensis*, and the tucuxi, *Sotalia fluviatilis*. Incidental gillnet mortality of tens of thousands of franciscanas, *Pontoporia blainvillei*, over the last 40 years off southern Brazil, Uruguay, and northern Argentina may have had a significant impact on this species.

Hector's dolphin, *Cephalorhyncus hectori*, inhabits the coastal waters of New Zealand. The total population may consist of only a few thousand individuals. In recent years, Hector's dolphins have been caught incidentally in gillnet fishing operations. Some scientists believe that the population has been significantly reduced. This species is highly vulnerable because of its relatively small population size, coastal habitat, and continuing incidental mortality that may exceed net recruitment in all or part of the species' range.

There may be tens of millions of spinner dolphins, *Stenella longirostris* and *S. clymene*, throughout the tropical waters of the world, but some local populations are declining. A morphologically distinct population known as the "eastern spinner" has been greatly reduced in the eastern tropical Pacific Ocean. Incidental catches of this population in the tuna purse-seine fishery have reduced it to about 20 percent of its original size over the last two decades—declining from about 2,000,000 to 400,000. Although the population is protected by the U.S. government under the Marine Mammal Protection Act (MMPA), U.S. fishermen are allowed to kill 2,750 per year, and many more are killed each year by non-U.S. tuna boats operating in the eastern tropical Pacific.

A hand harpoon fishery for Dall's porpoise in Japanese waters landed between 5,000 and



The boto, a South American river dolphin, is threatened by development of the Amazon basin.

9,000 animals annually during the 1960s and '70s. In recent years this fishery has expanded to meet the increased demand for porpoise meat. The annual catch is now between 10,000 and 13,000 individuals. This catch is 10 percent or more of the total number of Dall's porpoises—about 100,000 individuals—known to migrate through the fishing ground. Tomio Miyashita and Toshio Kasuya of the Far Seas Fisheries Research Laboratory in Japan are concerned, as are we, that the continuation of the harpoon fishery at such high levels will further deplete Dall's porpoise populations. An unknown but presumably large number of porpoises is also caught incidental to Japanese, Taiwanese, and Korean drift-gillnet fisheries for salmon and squid in the North Pacific.

The number of endangered cetacean populations continues to grow as more data are collected, yet these species have seldom been given adequate recognition or protection. Some additional populations at risk are listed in Table 3.

A Strategy for Cetacean Conservation

We propose a three-part strategy for cetacean conservation as follows:

EVALUATE THE STATUS OF ALL SPECIES

For the last 25 years, conservation biologists have described the status of the world's biota by compiling lists that have included only those species definitely known to be in trouble. Christoph Imboden, Director of the International Council for Bird Preservation in Cambridge, England, has pointed out that this strategy was a major error, because many people have assumed that any species not included on these lists is in no danger.

This assumption is false. Conservation biologist Jared M. Diamond, of the University of California at Los Angeles, has summarized recent surveys of birds and bats on tropical islands. His summary reveals that many species never included on endangered species lists because of insufficient data are now extinct. Because there are so many other species whose present status is unknown, but that may be endangered, Imboden and Diamond suggest that conservationists should also compile "Green Lists" (in contrast to the IUCN's Red List) that include only those species in no danger of extinction.

For cetaceans, we suggest a Green List of those species and populations known to be secure, a Red List of those known to be threatened or endangered, and a Gray List of those that may be threatened or endangered but whose true status is unknown. Margaret Klinowska (article, pp. 19–20) of Cambridge University is working on a new IUCN Red Data Book for cetaceans. It will evaluate the status of each species, rather than just those the IUCN currently recognizes as endangered, vulnerable, or insufficiently known.

REVISE ENDANGERED SPECIES LISTS

The present U.S. Threatened and Endangered Species List under the ESA lacks international scientific and political credibility with respect to cetaceans. It includes some species that are in no danger, and fails to include others that are nearly extinct or severely threatened. Revising this list to reflect the actual status of the world's cetaceans would make it a more valuable conservation tool.

Species of whales with large and increasing populations that are no longer commercially exploited are not endangered according to the present definition of "endangered" under the ESA or any other reasonable definition of the word. Some cetaceans listed as endangered, such as the sperm whale and the California gray whale population, do not even meet the less stringent criterion for "threatened" status.

The present status of the great whales is more accurately reflected by the Red List maintained by the IUCN. It now lists only four of the great whales as endangered in its Red List: the blue, bowhead, northern right, and humpback whales. The IUCN also lists the fin and the southern right whales as "vulnerable," a

Table 2. Criteria for listing a species (or population) as "threatened" or "endangered" under the U.S. Endangered Species Act. Only one criterion need apply for a species to be listed in either category.

1. **The present or threatened destruction, modification, or curtailment of habitat or range.**
2. **Overutilization for commercial, recreational, scientific, or educational purposes.**
3. **Disease or predation.**
4. **Inadequacy of existing regulatory mechanisms.**
5. **Other natural or manmade factors affecting its continued existence.**

Uruguayan fishermen set gillnets for sharks, but many porpoises and seals become accidentally entangled in the nets. The franciscanas being carried off at right may wind up as pig food or be rendered for oil.

category similar to the threatened category in the U.S. system; it does not list the gray, sperm, or sei whales in either category. However, the IUCN system also has some shortcomings, particularly in failing to recognize and classify threatened populations of species that are not threatened as a whole. Some of these threatened populations are identified in the Cetacean Action Plan recently developed by the Cetacean Specialist Group of the IUCN's Species Survival Commission. This action plan could be used as a starting point for updating the IUCN list.

We believe it is past time to reassess both the Red List and the U.S. Endangered Species List. We recommend that the U.S. government and the nongovernmental conservation organizations recognize the conservation victories that have been achieved for the sperm whale and the California gray whale population by supporting their removal from the ESA List. (The Korean gray whale population, of course, should be listed as endangered.) We also recommend an in-depth review of the present status of the other large whale populations with respect to the listing factors specified under the ESA. Such a review might result in additional species, such as the fin and sei whales, being delisted or downgraded from the endangered to the threatened category.

The delisting of no-longer-threatened species or populations would help focus attention on those great whales whose populations are still at critically low levels, such as the two species of right whales and most bowhead whale populations. Delisted species would still retain adequate legal protection under The Convention on International Trade in Endangered Species, which prohibits all trade in products derived from cetaceans. In addition, all cetacean populations in U.S. waters would still be protected by the MMPA.

Some conservationists oppose delisting any of the great whales. They argue that although these species are no longer threatened by the factors that led to their original listing, present human activities may threaten them in the future. They fear that someday the IWC may allow the resumption of commercial whaling on some species or stocks and that the oil and gas exploration now under way at many locations along the world's continental shelves could seriously harm whales that use these coastal areas. However, these possible threats are not sufficient to justify listing a species according to the factors that must be considered under the ESA. If they were, the majority of the world's animals would have to be included on the list—vast numbers of species are potentially threatened by the explosive growth of human populations, current rates of habitat destruction, and other harmful activities.

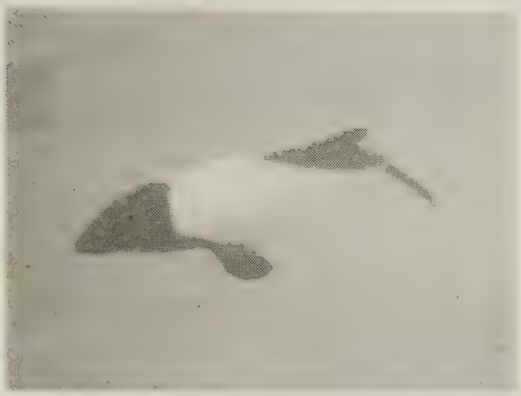
In addition to delisting nonendangered species, it is imperative to list truly endangered species. Among the small cetaceans, highest priority should be given to the baiji. A petition to add this species is already under review by NOAA Fisheries. Another species being reviewed by NOAA Fisheries, the Indus river dolphin, also deserves listing, as does the "eastern spinner" dolphin population. Listing these small cetaceans could provide the stimulus for the U.S. government to enter into bilateral agreements, under the ESA and the MMPA, for research and conservation in waters outside U.S. jurisdiction. Amendments to the Foreign Assistance Act in 1983 and 1986 require the U.S. government to support financially the conservation of endangered species and their habitats through the Agency for International Development.

Many other species and/or populations of small cetaceans may be in trouble, but insufficient data are available to support a petition to list them. The species that the IUCN includes in its "insufficiently known" category are the franciscana, the Irrawaddy dolphin (*Orcaella brevirostris*), the beluga (*Delphinapterus leucas*), the narwhal (*Monodon monoceros*), the harbor porpoise (*Phocoena phocoena*), the black dolphin (*Cephalorhynchus eutropria*), Commerson's dolphin (*C. commersonii*), Heaviside's dolphin (*C. heavisidii*), and Hector's dolphin. These animals should be studied and listed if sufficient data become available. As more small cetaceans are listed, their true status will be better understood by both government managers and nongovernmental conservation organizations.

REFOCUS CONSERVATION EFFORTS
Because many people are unaware of the true status of various cetacean species and populations present conservation efforts are not focused on the species most in need of help. Those people who are more informed about the actual status of cetaceans should strive to inform and educate government agencies, nongovernmental conservation organizations, and the general public. Once people are aware of the true threats, they can work together to initiate international research projects on the population trends and habitat needs of each species. The Cetacean Action Plan, for instance, lists specific needs for various species and populations.

Increased Credibility

Although many people throughout the world support the conservation of whales, dolphins, and porpoises, the energy and funds available for this purpose are in short supply relative to need. Adoption of the three-part strategy we have presented should lead to better use of these limited resources by enhancing the credibility of the available data and lists, and the corresponding recommendations for the conservation of cetaceans. This strategy will also help to concentrate efforts where they are most needed. □



Commerson's dolphin, found only in the waters off the southern part of South America.

Selected References

Breiwick, J. M., and H. W. Braham, eds. 1984. The status of endangered whales. *Mar. Fish. Rev.* 46(4):1–64.

Diamond J. M. 1988. Red books or green lists? *Nature* 332:304–305.

IUCN. 1988. *1988 Red List of Threatened Animals*. 154 pp. Gland, Switzerland: IUCN.

Leatherwood, S., R. R. Reeves, and L. Foster. 1983. *The Sierra Club Handbook of Whales and Dolphins*. 302 pp. San Francisco: Sierra Club Books.

Perrin, W. F. 1988. *Dolphins, Porpoises, and Whales—An Action Plan for the Conservation of Biological Diversity: 1988-1992.* 30 pp. Gland, Switzerland: IUCN.

Perrin, W. F., R. L. Brownell, Jr., K. Zhou, and J. Liu (eds.). 1989. *Biology and Conservation of the River Dolphins*. IUCN Species Survival Commission Occasional Paper 5. Gland, Switzerland: IUCN.

Table 3. Populations at risk (within species not threatened as a whole), based on the recent IUCN action plan for cetaceans.

Species	Location of Population(s)
Dall's porpoise, *Phocoenoides dalli*	**Northern Japanese waters**
Burmeister's porpoise, *Phocoena spinipinnis*	**Peruvian waters**
Dusky dolphin, *Lagenorhynchus obscurus*	**Peruvian waters**
Peale's dolphin, *Lagenorhynchus australis*	**Chilean and Argentine waters**
Finless porpoise, *Neophocaena phocaenoides*	**Yangtze River and Chinese coasts**
Atlantic humpbacked dolphin, *Sousa teuszii*	**West African coasts**
Bottlenose dolphin, *Tursiops truncatus*	**Black Sea**
Common dolphin, *Delphinus delphis*	**Black Sea**
Spinner dolphin, *Stenella longirostris*	**Sri Lankan coasts, Indian Ocean, and eastern tropical Pacific**
Risso's dolphin, *Grampus griseus*	**Sri Lankan coasts, Indian Ocean**
Pantropical spotted dolphin, *Stenella spp.*	**Sri Lankan coasts, Indian Ocean**
Striped dolphin, *Stenella coeruleoalba*	**Sri Lankan coasts, Indian Ocean**
Long-finned pilot whale, *Globicephala melas*	**Waters around the Faroe Islands**
Indio-Pacific humpbacked dolphin, *Sousa chinensis*	**All populations**
Short-finned pilot whale, *Globicephala macrorhynchus*	**Northern Japanese waters**
Baird's beaked whale, *Berardius bairdii*	**Northern Japanese waters**

Oops! On pages 4 and 5 of Vol. 32, No 1, because of editing errors, the IWC's 1982 moratorium on commercial whaling was said to be ending in 1991. In fact, the moratorium will be reviewed by 1991, and it will end only if a three-quarters majority votes to end it. Given the largly conservationist composition of the Commission, this highly unlikely.

8914

Growth During the Larval and Juvenile Stages of the Northern Anchovy, *Engraulis mordax*, in the California Current During 1980–84

John L. Butler

ABSTRACT: Increment widths and back-calculated growth rates for northern anchovy, *Engraulis mordax*, did not differ during the years 1980–84. This evidence of stable larval growth rates does not support the theory that it is the variation in larval growth rates that directly affects the magnitude of recruitment. Furthermore, since growth rates remained stable, even though zooplankton volumes in 1983 were well below the long-term mean, it follows that surviving post-first-feeding larval anchovies may not be food limited.

The size of juvenile northern anchovy was reduced during the 1982–83 El Niño "phenomenon" in the California Current. Mean lengths of anchovy juveniles collected in the fall were greatest in 1980, least in 1982, and intermediate in 1981, 1982, and 1984. Growth rates back calculated from otolith increment widths did not differ significantly between the 1980 and 1983 cohort, until 100 days after first feeding. Reduced growth after 100 days largely determined the smaller size of 1983 anchovy juveniles. Condition factor was also reduced in the 1983 cohort. The 1982 cohort was not greatly affected, because El Niño did not have a pronounced effect off the North American coast until well after the 1982 northern anchovy spawning season.

Through the years, the overall abundance of many pelagic fishes varies with the strength of individual year class; changes in mortality rates early in life (Hjort 1914, 1926), rather than parent stock size, may determine the size of individual year classes. Considerable controversy, however, surrounds details of the exact stage and mechanism through which changes in individual year-class strength occur.

The co-occurrence of fish larvae and their food is a mechanism that has been proposed to explain variations in year-class strength (Hjort 1914, 1926). Lasker (1978) has shown that food availability may affect survival of first-feeding northern anchovy, *Engraulis mordax*, larvae in the sea. Food availability may not affect the survival beyond the first-feeding stage; however, Methot (1981) found that early larval anchovy growth rates in the sea were the same as those of well-fed, laboratory-reared larvae. Survival through the larval stage does not determine the magnitude of the northern anchovy recruitment (Peterman and Bradford 1986; Peterman et al. 1988). Thus food availability for larvae may not determine the year-class strength and whether food availability affects juvenile survival are yet to be investigated.

A simulation model of the northern anchovy population indicates that the growth rate of late larvae and early juveniles may affect the magnitude of recruitment (Smith 1985). If mortality rates in the marine environment are size-specific, as predicted by Peterson and Wroblewski (1984), and if growth rates determine the duration of the most vulnerable stages, reduced growth should adversely affect survival. The extent to which growth rates of late larvae and juveniles vary is unknown.

The growth rate of juveniles also affects adult size. Off southern Baja California, the adult size of northern anchovy is entirely determined by juvenile growth, because these fish show no growth after 18 months (Parrish et al. 1985). Analysis of the regional patterns of growth of northern anchovy shows that the average length of fish at a given age increases from south to north. The length at 18 months ranges from 101.1 mm off southern Baja California to 126.6 mm off central California (Parrish et al. 1985).

Because batch fecundity is a function of body size in broadcast spawners, the juvenile and adult growth rates determine the reproductive capacity over the adult lifespan. Competition among juveniles for resources affects adult fertility in other species (Prout and McChesney 1985), and, if growth of juvenile pelagic fishes is food limited, competition among juveniles may

---

John L. Butler, Southwest Fisheries Center, National Marine Fisheries Service. NOAA, P.O. Box 271, La Jolla, CA 92038.

Manuscript Accepted April 1989.
Fishery Bulletin, U.S. 87: 645–652.

be a mechanism of density-dependent compensation.

Growth rates of larval and juvenile anchovy during El Niño periods are of particular interest, because the growth rates during an environmental perturbation may reveal details of the processes of growth and survival during normal conditions. During the 1982–83 El Niño event off California, temperatures were elevated (Lynn 1983; Simpson 1983) and zooplankton density was reduced in 1983 (McGowan 1985). If planktivorous fish compete for food, competition should be highest when zooplankton abundance is lowest. Comparison of growth rates throughout the larval and juvenile stages during periods of low and high food abundance may show the size range at which the larval or the juvenile stage is most important. In this paper I examine the interannual variability in growth rates of anchovy larvae and juveniles during periods of low and high food abundance.

METHODS

Samples of juveniles from the central population of northern anchovy were obtained from midwater trawl hauls taken in 1980–84 by the Sea Survey Program of the California Department of Fish and Game. Annual cruises to monitor the strength of the incoming year class of northern anchovy have been conducted during September and October since 1976; Mais (1974) has described the gear and sampling procedures. The surveys extended along the Pacific coast from central Baja California to Point Conception, CA, with the exception of 1982, when the southern limit was the U.S.-Mexican border. Trawl hauls were taken nearshore inside of a 75 fm contour where young of the year are most abundant during the fall (Parrish et al. 1985).

Twenty five juvenile northern anchovy were randomly taken from each positive trawl haul and frozen for age determination. A subsample of 200 juvenile anchovy was randomly taken from the 800 to 1,000 fish collected on each survey for analysis of growth rate using daily increments in the otoliths. Fish were measured from the tip of the snout to the posterior edge of the hypural plate (standard length), and otoliths were removed and mounted on microscope slides using Eukitt[1] mounting medium.

Growth rates and ages of juvenile northern anchovy were determined by counting and measuring daily increments in the otoliths (Methot 1981). The increment widths were measured and recorded along a transect from the focus to the posterior margin of the otolith (otolith radius), using a video-coordinate digitizer connected to a microcomputer. The otoliths were progressively polished between readings, using 15 and 0.3 μ lapping film, to reveal increments along the entire transect. Data from different areas of the otolith were collected as the increments became visible. During each reading groups of 10 or less (typically five) increments were counted and measured. The number of increments measured was reduced if width varied among increments.

ANALYSIS AND RESULTS

Data from both otoliths and several replicate transects per otolith were combined to calculate age and otolith increment widths (Methot 1981). Mean increment width was calculated at each point along the radius from the focus to the posterior margin of the otolith. In some cases, it was impossible to obtain measurements of all increment widths in the otoliths. In these cases, increment widths were interpolated using linear approximation (see Methot 1983 for details). Data for increment widths and age estimates were not used if more than 5% of age was calculated from interpolated increments.

A direct comparison of the average size of recruits from year to year is inappropriate because their ages may differ from year to year owing to differences in the dates of spawning (Methot 1983) or to dates of collection. To eliminate this bias, the dates of hatching were determined from the dates of sampling and ages, and fish were grouped by year and month of hatching.

Interannual and seasonal differences in length were tested, using an analysis of covariance (Bartlett et al. 1984) with age as the covariate. This analysis adjusted the mean length to the grand mean age of 208 days, approximately the time elapsed from the peak of spawning to the date of capture. Since the relation of length to age is typically nonlinear, some error is introduced using a linear adjustment. The difference in dates of sampling is, however, only about one month and the relation of size to age is approximately linear from two to six months.

Analysis of covariance of these data indicates parallel lines with differences in means (Case 2c in Bartlett et al. 1984). Thus, comparison of lengths adjusted by age between years of fish hatched during the same calendar month is reliable. Comparison of lengths of fish hatched at the extremes of the same spawning season may be less reliable than between-year comparisons. Fish hatched in January are four months older than fish hatched in May, and linear extrapolation to a common age may introduce error. However, since growth is decelerating, linear extrapolation overestimates mean lengths of fish hatched at the extremes of the spawning season. The fact that lengths of fish hatched in January and May in all years, except 1983, are less than lengths of fish hatched in March indicates that the error is not great.

---

[1] Reference to tradenames does not imply endorsement by the National Marine Fisheries Service, NOAA.

The allometric relations of length and weight to otolith radius were estimated using nonlinear regression. These relations were used to back-calculate age-specific size and growth rates for individual fish; not all fish were weighed in 1980 and 1981, and data were pooled from 1980 to 1982 to determine the allometric relations of both length and weight to otolith radius. Individual relations were determined for 1983 and 1984.

The growth rates in length and in weight were determined from increment widths and the first derivative of the empirical relationship of fish size and otolith radius. The condition factor (dry weight/length cubed) was significantly less in anchovy juveniles collected in 1983 than in anchovy juveniles collected in 1980–82. Therefore, the algorithm to convert otolith increment size to growth in dry weight differed among years. The equation used to calculate growth in length was

$$\Delta L/\Delta t = (\Delta R/\Delta t)(\Delta L/\Delta R); \qquad (1)$$

where $\Delta R/\Delta t$ is rate of change of the width of the daily increments, and $\Delta L/\Delta R$ is the slope of the observed relationship of fish length and otolith radius.

The variance of the product (Y) of two variables (X, Z) is given by

$$\mathrm{Var}(Y) = Z^2\mathrm{Var}(X) + X^2\mathrm{Var}(Z) + 2XZ\,\mathrm{Covar}(XZ) \qquad (2)$$

if the variables are not independent (Goodman 1960). The estimate of the variance of $\Delta R/\Delta t$ was the variance of the measurement of increment width of the fish in each group. If the length, radius relation was linear, the variance of $\Delta L/\Delta R$ was estimated from $S^2_{Y|X}$, the variance of the slope of the regression of length on otolith radius. If the relation of length to radius was nonlinear, as was often the case, the variance of $\Delta L/\Delta R$ was estimated by partial derivatives. The variance of $\Delta W/\Delta R$ was not calculated; the complex derivative may not be a good estimate of the true variance.

The author tested the assumption that the covariance was equal to zero by comparing the slopes of the relations of juvenile fish length and otolith radius for 70–100 mm, slow- and fast-growing fish collected in October 1984 that were ≥ 1 year old. The slope was 0.0419 for anchovy older than one year and 0.0314 for fish younger than one year old. These slopes were not significantly different ($P > 0.10$, ANCOVA). Consequently confidence intervals around back-calculated growth rates were calculated ignoring the third term in Equation (1).

Lengths of anchovies were significantly different between months and years ($P < 0.01$, ANCOVA). Within a spawning season, fish hatched during February, March, and April grew faster than fish hatched in January or May (Fig. 1), although this was not evident for the 1983 or 1984 data. The mean of five fish in January 1982 was not different from that of the April 1982 sample. The adjusted lengths of juveniles collected from the 1983 year class where less than the adjusted lengths of any of those from 1980–82 for all months but May (Fig. 1, Table 1). The adjusted lengths of juveniles from

TABLE 1.—Mean lengths at capture of juvenile northern anchovy hatched in various months of 1980–84, adjusted to a common age of 208 days. SE and *N* stand for standard error and number of fish, respectively.

	Month of Hatching				
Year	Jan.	Feb.	Mar.	Apr.	May
1980	71.4	78.7	84.6	83.6	72.3
SE	3.6	1.6	1.0	1.6	
N	7	30	104	33	2
1981	77.0	79.9	83.5	82.7	79.7
SE	2.2	2.2	1.2	1.5	2.4
N	21	29	42	35	16
1982	81.1	85.79	84.1	81.0	78.9
SE	4.5	1.3	1.1	1.2	1.6
N	2	32	70	53	29
1983	70.0	71.4	71.5	70.8	73.7
SE	2.6	2.1	0.9	0.9	2.7
N	9	17	99	45	8
1984	74.8	77.0	76.0	76.8	75.6
SE	1.5	1.3	1.3	1.9	1.5
N	39	53	42	22	17

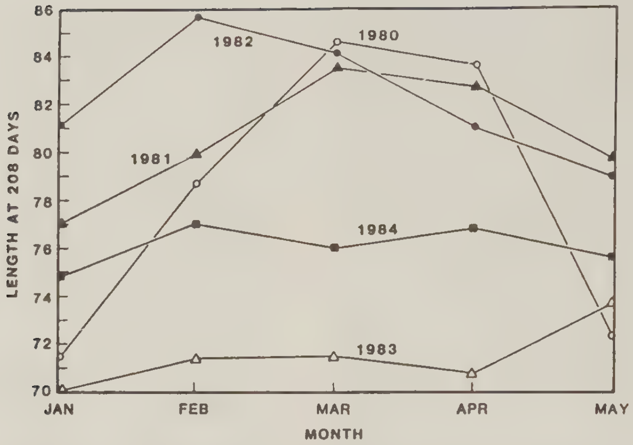


FIGURE 1.—Mean lengths adjusted for age of northern anchovy spawned in 1980–84. For each year, fish are grouped by back-calculated date of hatching, and length at capture is adjusted to mean age of 208 days.

1984 were intermediate between those of 1980–82 and 1983.

Fish hatched during 1983 did not grow more slowly throughout the entire larval and juvenile stage than during other years. Otolith increment widths from 104 juveniles hatched in March 1980 were compared with otolith increment widths from 99 juveniles hatched in March 1983 (Fig. 2). In fish smaller than 40 mm in length, increment width was not different. Above 40 mm, the otolith increment widths were smaller in the 1983 sample than in the 1980 sample ($P < 0.01$); the 95% confidence limits for the two cohorts did not overlap. These results show that the difference in lengths of the two cohorts indicated by the analysis of covariance is largely due to difference in growth rate after a size of 40 mm, rather than to a reduction of growth throughout life.

Back-calculated lengths and growth rates of 1980 northern anchovy juveniles were greater

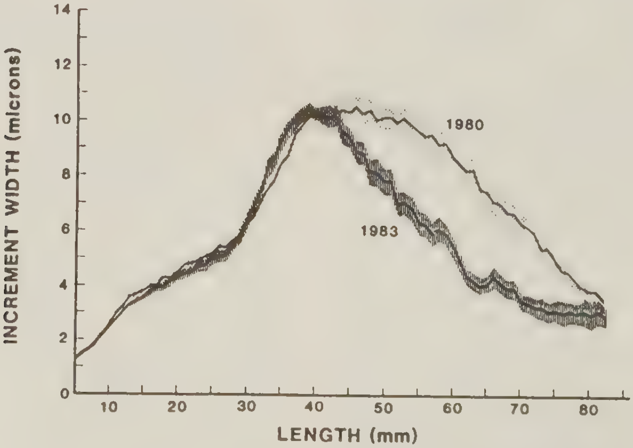


FIGURE 2.—Average otolith increment width versus length of 104 northern anchovy spawned in March 1980 and of 99 anchovy spawned in March 1983. Shaded areas are 95% confidence intervals.

than those of 1983 (Figs. 3, 4). Cohorts did not differ significantly in growth until approximately 40 mm. The age of the end of the late larval (10 mm) period was 20 days in 1980 and 19 days in 1983. A local minimum for growth rates of 1983 fish occurred at about 35 mm and at about 42 mm for growth rates of 1980 fish. This corresponds, approximately, to metamorphosis from late larval stage to juvenile stage. The duration of the late larval period (10–35 mm) was about 70 days in both 1980 and 1983.

After metamorphosis, growth rates increased in 1980 and 1983 until about 40 mm. At about 40 mm, the growth rates of the two cohorts diverged, and the mean back-calculated growth rate of the 1983 cohort was well below the estimated 95% confidence interval of the 1980 cohort. Growth rates declined steadily in 1983 at sizes larger than 40 mm, while growth rates of about 0.4 mm/d were sustained in 1980 until almost 60 mm. After 60 mm, growth declined at about the same rate as the decline in the 1983

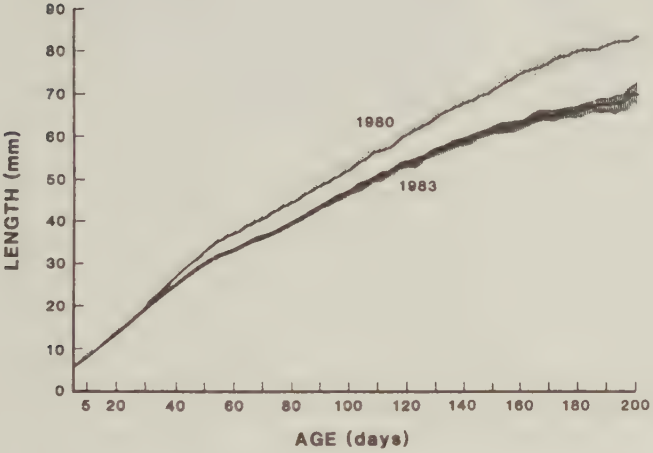


FIGURE 3.—Length versus age of northern anchovy larvae and juveniles of the March 1980 and 1983 cohorts back calculated from daily increments in otoliths.

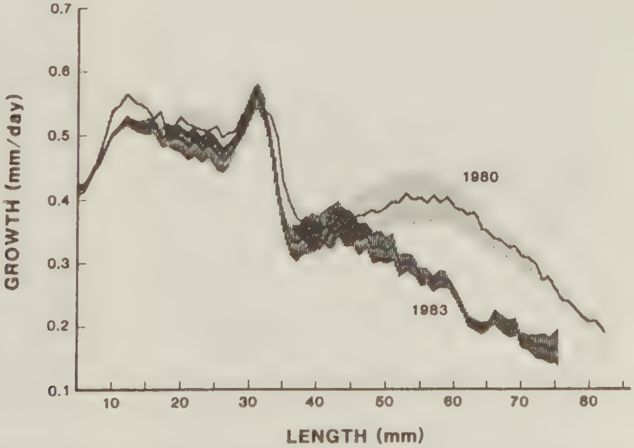


FIGURE 4.—Age-specific growth rates back calculated from daily increment widths of northern anchovy spawned in March 1980 and March 1983. Growth rate of length in mm per day. Shaded areas are 95% confidence intervals.

cohort. Growth within cohorts varied most between 40 and 60 mm.

In 1980 and 1983, northern anchovy growth in weight increased rapidly at small sizes (Fig. 5). Back-calculated growth rates for 1983 reached a local maximum of 6.5 mg/d at about 40 mm and then declined before slowly increasing to 7.5 mg/d at 79 mm. Back-calculated growth rates for 1980 showed a steady increase to about 11.5 mg/d at about 65 mm, which was maintained until about 75 mm, after which growth declined. The growth of northern anchovies hatched in March 1983 peaked at an earlier time (about June) in 1983 and at a smaller size (40 mm), whereas the growth of anchovies hatched in March 1980 peaked near the end of July 1980 and at a larger size at (about 65 mm).

geographic shifts in the population or to changes in spawning date and sampling time in 1984.

When size is adjusted for age and date of spawning, growth of juvenile northern anchovy was reduced in fish hatched in February through April of 1984 compared with fish hatched in the same months in 1980–82 (Fig. 1). This result is consistent with the results from studies of other fish populations on the west coast during El Niño. Growth rates and condition factors were also reduced in the Pacific herring, *Clupea harengus pallasi* (Spratt 1987), the blue rockfish, *Sebastes mystinus* (Van Traskie[2]), and in chinook, *Onchorhynchus tshawytscha*, and coho, *Onchorhynchus kisutch*, salmon (Pearcy and Schoener 1987) during El Niño.

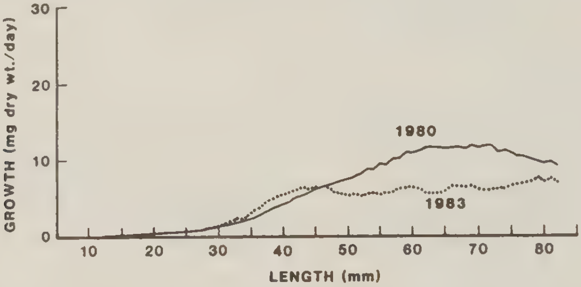


FIGURE 5.—Mean back-calculated growth rates of northern anchovy spawned in March 1980 and March 1983. Growth rate of mass in mg dry weight per day.

DISCUSSION

Growth rates of late larval northern anchovy did not vary in two otherwise extreme years, 1980 and 1983. Methot (1981) found little variance in early larval growth in the sea. Smith (1985) postulated that major changes in recruitment would result from changes in growth rates in the late larval period (10–35 mm) from 0.227 to 0.559 mm/d, a difference of 0.3 mm/d. In this study, however, growth rates of the late larval stage varied by <0.05 mm/d between 1980 and 1983.

Northern anchovy juveniles grew less during 1983 and 1984, compared with the previous three years. Fiedler et al. (1986) also reported reduced growth of anchovy in 1983, but the mean size of 1 yr old fish indicated a dramatic recovery in 1984. This apparent recovery may be in part due to

Although the 1982–83 El Nino was fully developed by October 1982 along the coast of Peru, full development of large scale warming off the North American coast did not occur until January 1983 (Lynn 1983). Positive temperature anomalies (>1°C) were evident both at the surface and at depth throughout the California Current (McGowan 1985; Norton et al. 1985). Negative salinity anomalies associated with subsurface temperature anomalies indicated intrusion of low salinity water from the south and west into the Southern California Bight (Simpson 1983).

These temperature anomalies represent a large change in the heat content of the ocean but are small relative to the thermal range of northern anchovy. Thus the small size of juvenile anchovies during 1983 may be a direct result of reduced food availability at the same time that the rapidly growing juveniles experienced higher metabolic rates due to the elevated environmental temperatures. Zooplankton volumes on CalCOFI line 90 (line 90 intersects the coast at lat 33°29.9′N, long. 117°44.4′W and proceeds seaward on a bearing 240° clockwise from North) were lower than the 95% confidence limit of the 30 year CalCOFI time series (McGowan 1985).

---

[2] Van Traskie, D. 1985. Growth of blue rockfish (*Sebastes mystinus*) during El Niño. (Abstr.) Calif. Coop. Fish. Invest. Conf., Idyllwild, CA, Oct. 22–25, 1985.

Growth rates were not, however, depressed over the entire early life history. The growth rates of larval stages (5–35 mm) were not significantly different between the two years 1982–83 (Figs. 3, 4). Growth rates in 1983 were reduced in the early juvenile stage, and in particular after 40 mm, compared with growth rates in 1980.

Thus food was not growth limiting until the fish reached a certain size. As fish larvae grow, the ration necessary to sustain growth increases. Since the density of food particles decreases with size (Sheldon and Parsons 1967; Sheldon et al. 1972), at some stage food must become growth limiting. Based on this analysis, food-limited growth is unlikely in anchovies <40 mm during conditions that existed in the Southern California Bight in 1983, and unlikely in anchovies <65 mm during "normal" years such as 1980.

The similarity of back-calculated larval growth rates between years may be a result of the interaction of growth and mortality. A wide range of growth rates are possible at this stage (Hunter 1980), but variable growth rates are not observed in the field. Mortality of slow-growing individuals may reduce the range of growth rates in survivors to metamorphosis.

While the 1957–58 El Niño had a dramatic effect on northern anchovy recruitment in 1958, the numbers of fish in the 1983 and 1984 year classes were not appreciably lower than the previous years (Methot 1988). Thus, although the juvenile period was prolonged in 1983, recruitment was not affected. The major effect of El Niño on the anchovy population was to reduce the size of recruits as well as perhaps the size of adults and the reproductive potential of the 1983 and 1984 cohorts.

ACKNOWLEDGMENTS

I am indebted to Dr. Reuben Lasker (National Marine Fisheries Service, NOAA) for many thought provoking discussions. Ken Mais (California Department of Fish and Game) provided samples of juvenile anchovy from survey cruises. Susan Longinotti (University of California at San Diego) collected much of the data analyzed here. John R. Hunter, Paul E. Smith, and Robert W. Owen of the National Marine Fisheries Service and William H. Bayliff of the Inter-American Tropical Tuna Commission made many useful comments on the manuscript.

LITERATURE CITED

Bartlett, J. R., P. F. Randerson, R. Williams, and D. M. Ellis.
1984. The use of analysis of covariance in the back-calculation of growth in fish. J. Fish Biol. 24:201–203.

Fiedler, P., R. D. Methot, and R. Hewitt.
1986. Effects of California El Nino 1982–1984 on the northern anchovy. J. Mar. Res. 44:317–338.

Goodman, L. A.
1960. On the exact variance of products. J. Am. Statist. Assoc. 55:708–713.

Hjort, J.
1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-v. Réun. Cons. int. Explor. Mer 20:1–228.
1926. Fluctuations in the yearclasses of important food fishes. J. Cons. int. Explor. Mer 1:5–38.

Hunter, J. R.
1980. Culture and growth of northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 79:215–230.

Lasker, R.
1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp. P.-v. Réun. Cons. int. Explor. Mer 173:212–230.

Lynn, R. J.
1983. The 1982–83 warm episode in the California Current. Geophys. Res. Let. 10:1093–1095.

Mais, K.
1974. Pelagic fish surveys in the California Current. Calif. Dep. Fish Game Fish Bull. 162:1–79.

McGowan, J. A.
1985. El Niño 1983 in the Southern California Bight. *In* W. S. Wooster and D. L. Fluharty (editors), El Niño North, Niño effects in the Eastern Subarctic Pacific Ocean, p. 166–187. Wash. Sea Grant, Seattle, WA.

Methot, R. D.
1981. Growth rates and age distributions of larval and juvenile northern anchovy, *Engraulis mordax*, with inferences on larval survival. Ph.D. Thesis, Univ. California, San Diego, CA, 209 p.
1983. Seasonal variation in survival of larval northern anchovy, *Engraulis mordax*, estimated from the age distribution of juveniles. Fish. Bull., U.S. 81:741–750.
In press. Synthetic estimates of historical abundance and mortality for northern anchovy. *In* E. F. Vetter and B. A. Megrey (editors), Mathematical analysis of fish stock dynamics. Am. Fish. Soc. Symp. Vol. Ser.

Norton, J., D. McLain, R. Brainard, and D. Husby.
1985. The 1982–83 El Niño event off Baja and Alta California and its ocean climate context. *In* W. S. Wooster and D. L. Fluharty (editors), El Niño North, Niño effects in the Eastern Subarctic Pacific Ocean, p. 44–72. Wash. Sea Grant, Seattle, WA.

Parrish, R. H., D. L. Mallicoate, and K. F. Mais.
1985. Regional variations in the growth and age composition of northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 83:483–496.

Pearcy, W. G., and A. Schoener.
1987. Changes in the marine biota coincident with the 1982–83 El Niño in the Northeastern Subarctic Pacific Ocean. J. Geophys. Res. 92:14417–14428.

Peterman, R. M., and M. J. Bradford.
1987. Wind speed index correlates with mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*). Science 235:354–366.

Peterman, R. M., M. J. Bradford, N. C. H. Lo, and R. D. Methot.
1988. Contribution of early life stages to interannual variability in recruitment of northern anchovy (*Engraulis mordax*). Can. J. Fish. Aquat. Sci. 45:8–16.

Peterson, I., and J. S. Wroblewski.
1984. Mortality rate of fishes in the pelagic ecosystem. Can. J. Fish. Aquat. Sci. 41:1117–1120.

Prout, T., and F. McChesney.
1985. Competition among immatures affects their adult fertility: population dynamics. Am. Nat. 126:521–558.

Sheldon, R. W., and T. R. Parsons.
1967. A continuous size spectrum for particulate matter in the sea. J. Fish. Res. Board Can. 24:909–915.

Sheldon, R. W., A. Prakash, and W. H. Sutcliffe, Jr.
1972. The size distribution of particles in the ocean. Limnol. Oceanogr. 17:327–340.

Simpson, J. J.
1983. Large-scale thermal anomalies in the California current during the 1982–1983 El Niño. Geophys. Res. Lett. 10:937–940.
1984. El Niño induced onshore transport in the California Current during 1982–1983. Geophys. Res. Lett., 11:241–242.

Smith, P. E.
1985. Year-class strength and survival of 0-group clupeoids. Can. J. Fish. Aquat. Sci. 42:69–82.

Spratt, J. D.
1987. Variation in the growth rate of Pacific herring from San Francisco Bay, California. Calif. Fish Game 73:132–138.

8915

JOURNAL OF CRUSTACEAN BIOLOGY. 9(4): 662–665. 1989

ACICONULA ACANTHOSOMA, NEW SPECIES, A CAPRELLID AMPHIPOD FROM SOUTHERN CALIFORNIA, WITH NOTES ON ITS ECOLOGY

James R. Chess

ABSTRACT

A caprellid amphipod, *Aciconula acanthosoma*, new species, is described from nearshore waters of Santa Catalina Island, California. Previously the genus *Aciconula* was monotypic, known only from the western Pacific species *A. miranda*. The new species was common and persistent during 15 years of sampling, and was found on 12 types of substrata and in the gut contents of eight species of fishes. It is distinguished from *A. miranda* primarily by the spination of the head and pereionites.

During studies of nearshore marine communities at Santa Catalina Island in southern California, I collected specimens of a caprellid amphipod referable to the genus *Aciconula*. It was common and persistent from 1973–1988 in samples from a variety of substrata, and in the gut contents of fishes. Subsequent study showed that these specimens differ from the unique type species *A. miranda* Mayer, 1903, known from six specimens from widely separated localities in the western Pacific Ocean (Arimoto, 1971). The new species is described herein.

Aciconula acanthosoma, new species
Figs. 1, 2

Type Material.—Holotype male, length 7.3 mm, on *Cystoseira neglecta* Setchell and Gardiner, 1917, depth 11 m, Isthmus Reef, Santa Catalina Island, California (33°23′N, 118°30.5′W), 25 August 1981, J. R. Chess collector, deposited in the National Museum of Natural History, Smithsonian Institution, Washington D.C., USNM 240206. Allotype female, length 6.2 mm, locality as for holotype, USNM 240207. Ten paratypes, locality as for holotype, USNM 240208.

Locality Records.—Large numbers of specimens were collected from several sites on the leeward side of Santa Catalina Island, primarily from Isthmus Reef, depth 11–14 m. Other Santa Catalina Island sites included Fisherman's Cove, depth 8 m; Lions Head Point, depth 12 m; and West End Point, depth 7 m. This amphipod was also reported from San Clemente Island (33°00′N, 118°33′W), depth and collection site unknown (Bruce Benedict, Marine Biological Consultants, Costa Mesa, California, personal communication, 1973).

Other Material.—30 specimens, 4.0–7.6 mm, from Isthmus Reef, Santa Catalina Island, California, 25 August 1981.

Diagnosis.—A species of *Aciconula* which has the following features: head with 4 prominent curved spines; all pereionites dorsally spinose; flagellum of antenna 1 with 10–12 articles; basis of gnathopod 2 with acute distolateral projection.

Description.—Male (length to 7.6 mm): Body dorsally spinose, 1 pair of spines on each pereionite flaring bilaterally; ventrolateral margins of pereionites 2–5 expanded laterally, spinose; pereionite 3 somewhat elongate, 2, 4, and 5 shorter and subequal. Antenna 1, flagellum with 12 articles. Antenna 2 exceeding peduncle of antenna 1; flagellum weakly setose, with 2 articles. Mandibular palp with 3 articles; terminal article with distal row of 8 blunt knobs and parallel row of 6 even spines with longer spine at each end. Mandibular molar large and ridged; lacinia mobilis of left mandible 5-denticulate, lacinia of right setulose, incisor strongly denticulate. Maxilla 1 endite with 6 terminal spines, palp with 4 terminal spines and single lateral seta. Maxilla 2 with few apical setae. Maxilliped inner lobe smaller than outer lobe and with 1 short tooth and 3 setae distally, palp article 4 with distal row of 5 setae. Gnathopod 1, propodus with 2 proximal grasping spines; propodus and carpus each with distal row of 6 setae on medial surface. Gnathopod 2, palmar surface of propodus with 2 distal triangular projections and medial excavation, bordered proximally by strong spine, proximal surface with row of fine blunt serrations and single grasping spine; basis with acute distolateral projection. Pereiopods 3 and 4 with 2 articles, article 2 of each conical, about one-half length of first, with 3 plumose apical setae. Pereionites 3 and 4 with gills. Pereiopod 5 unusual for caprellids but typical of genus, with 6 soft, flexible articles; articles 4 and 5 conspicuously setose, article 6 minute, none with grasping structures. Pereiopods 6 and 7 with 7 arti-

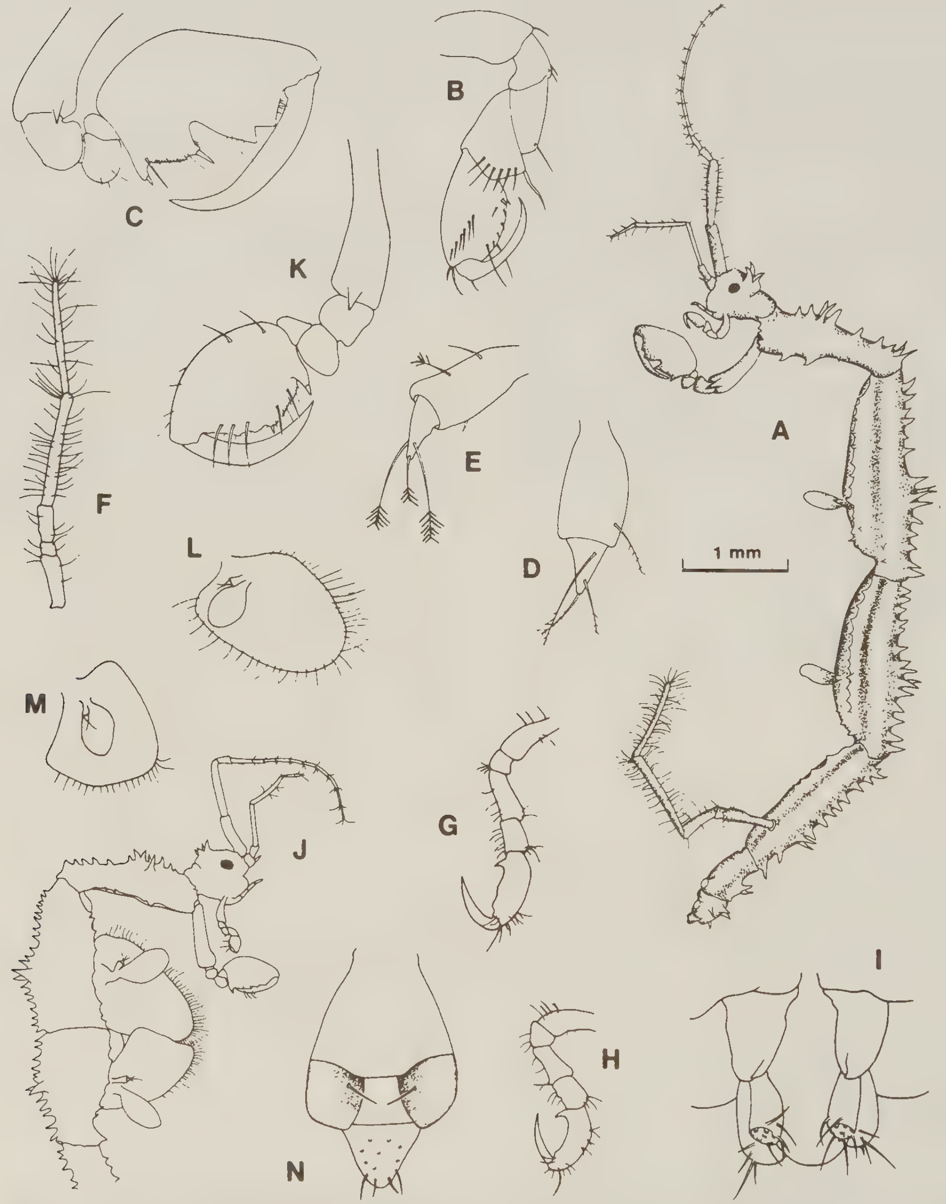


Fig. 1. *Aciconula acanthosoma*, new species, holotype, A–I, adult male. A, whole animal; B, gnathopod 1, medial view; C, gnathopod 2; D–H, pereiopods 3–7; I, abdomen. Allotype, J–N, adult female. J, anterior pereionites; K, gnathopod 2; L, M, oostegite, gill, pereiopods 3 and 4; N, abdomen.

cles, propodus of each with 1 pair of proximal grasping spines. Abdomen with penes lateral; distal end of appendages abruptly truncate with short multitipped terminal spines.

Female (length to 6.3 mm): Similar to male in spination and pereionite lengths. Antenna 1 with 10 articles; gnathopod 2 as figured; abdomen with 1 pair of posteriorly truncate lobes, each with medially directed seta, terminal protuberance punctate with 4 posterior setae.

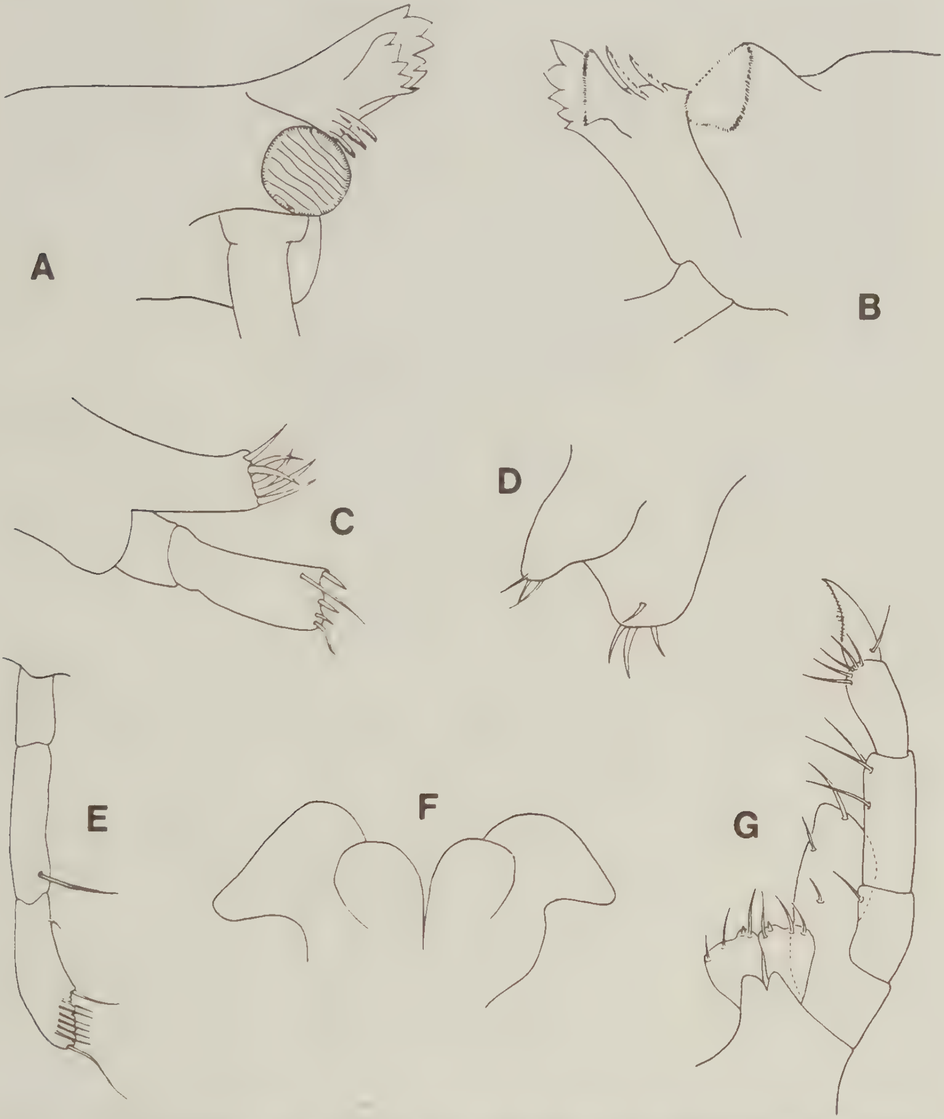


Fig. 2. *Aciconula acanthosoma*, new species, paratype, adult male. A, left mandible; B, right mandible; C, maxilla 1; D, maxilla 2; E, mandibular palp; F, lower lip; G, maxilliped.

Etymology.—From the Greek *acantha* meaning spine or thorn and *soma* denoting body.

Remarks.—*Aciconula acanthosoma* differs from *A. miranda* by the extensive spination of its head and pereion; by the inner lobe of the maxilliped being truncate and spinose, by the presence of the distal row of setae on article 4, and the setal formula 1:6:1 rather than 1:7:1 of the terminal article of the maxillipedal palp, and by the subequal lengths of pereiopods 3 and 4 (in *A. miranda* pereiopod 3 is approximately 3× the length of pereiopod 4).

Systematics.—McCain (1970) tentatively placed the genus *Aciconula* in the subfamily Protellinae within the Aeginellidae. His uncertainty arose from the lack of an appropriate description of the mandible of the type species. The presence of a mandibular molar, as well as the remaining characters of the Aeginellidae (the presence of a mandibular palp, reduced pereiopods 3 and 4, gills on pereionites 3 and 4, and an abdomen of a single reduced article) confirms his suspicion and allows familial placement of this genus.

Aciconula Mayer, 1903, was emended by Arimoto (1971) where he included several characters not considered in Mayer's original description. *Aciconula acanthosoma* conforms to all generic characters mentioned by Arimoto except the setal formula of the terminal article of the mandibular palp. This character does not constitute a generic difference.

Ecology.—Aciconula acanthosoma was found off the leeward (northern) shore of Santa Catalina Island within nearshore habitats that are protected from prevailing oceanic swells. The visually dominant feature of these habitats is narrow fringing beds of giant kelp, *Macrocystis pyrifera* (Linnaeus, 1771), with a benthic understory of foliose algae. *Aciconula acanthosoma* was found on 12 different substrata (of 21 examined) including sand, rock, the bryozoan *Bugula neritina* Linnaeus, 1758, the green alga *Codium fragile* (Suringar, 1867), the brown algae *Cystoseira neglecta, Desmarestia viridis* (Müller, 1782), *Dictyopteris undulata* Holmes, 1896, *Pachydictyon coriaceum* (Holmes, 1896), *Sargassum muticum* (Yendo, 1907), *Sargassum palmeri* Grunow, 1915, and *Zonaria farlowii* Setchell and Gardiner, 1924, and the red alga *Plocamium cartilagineum* (Linnaeus, 1753). The highest densities of *A. acanthosoma* (up to 70 individuals/100 g of algae) were found on *Cystoseira neglecta* and *Sargassum palmeri*, both perennial phaeophytes with relatively slender branching thalli. In contrast, foliose phaeophytes with broader thalli, such as *Dictyopteris undulata* and *Zonaria farlowii*, usually had much lower densities, about 15% of the former.

Aciconula acanthosoma was present during all seasons but was most abundant in February and March. Interannual variations in abundance tended to be greater than seasonal variations, with the lowest numbers occurring during and following the El Niño events of 1976 and 1983.

Stomach content analysis of predatory fishes from Santa Catalina Island revealed that *A. acanthosoma* was not a major dietary component in any of the species analyzed, but occurred infrequently in the diets of the cottid *Orthanopias triacis* Starks and Mann, 1911, the embiotocid *Embiotoca jacksoni* Agassiz, 1854, the pomocentrid *Hypsypops rubicunda* (Girard, 1854), the labrids *Halichoeres semicinctus* (Ayres, 1859) and *Semicossyphus pulcher* (Ayres, 1854), the clinid blenny *Alloclinus holderi* (Lauderbach, 1907), and the gobies *Coryphopterus nicholsi* (Bean, 1881) and *Lythrypnus zebra* (Gilbert, 1890).

The feeding mode of *A. acanthosoma* was investigated by study of gut contents from eight specimens. The only recognizable structures found were spicules of sponges and ascidians presumably scraped from substrata. The absence of diatom frustules in the gut contents, coupled with lack of well-developed setae on its second antennae, suggest that the species is not primarily a filter feeder (Caine, 1974).

Brooding females were found from January to March and the number of eggs per clutch appeared to be size-correlated, with the larger individuals carrying up to 14 eggs.

ACKNOWLEDGEMENTS

I thank Diana Laubitz (National Museums of Canada) for providing the generic designation, for clarifying various morphological features of the mandible, and for helpful comments on the manuscript. Henry Orr (Southwest Fisheries Center, NOAA) prepared the illustrations for publication.

LITERATURE CITED

Arimoto, I. 1971. Caprellidae of Japan (2).—Bulletin of the Biogeographical Society of Japan 26: 39–46.

Caine, E. A. 1974. Comparative functional morphology of feeding in three species of caprellids (Crustacea, Amphipoda) from the northwestern Florida Gulf coast.—Journal of Experimental Marine Biology and Ecology 15: 81–96.

McCain, J. C. 1970. Familial taxa within the Caprellidea (Crustacea: Amphipoda).—Proceedings of the Biological Society of Washington 82: 837–842.

Mayer, P. 1903. Die Caprellidae der *Siboga*- Expedition.—Siboga Expeditie 34: 1–160.

RECEIVED: 13 May 1989.
ACCEPTED: 22 June 1989.

Address: Southwest Fisheries Center, Tiburon Laboratory, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 3150 Paradise Drive, Tiburon, California 94920.

8916

TECHNIQUES

A NEW THERAPY FOR MARINE TURTLES PARASITIZED BY THE PISCICOLID LEECH, *Ozobranchus branchiatus*

Marine leeches, *Ozobranchus* spp., are prominent ectoparasites on the green turtle, *Chelonia mydas*, in the Hawaiian Islands and on certain other sea turtle populations worldwide (Hirth 1971; Balazs 1980). Both *O. branchiatus* and *O. margoi* have been documented on green turtles in Hawaii, but the former species is believed to be more prevalent (Balazs 1980). A quantitative survey on this subject is currently in progress by the authors.

The two species of leeches are easily distinguished in that *O. branchiatus* has seven pairs of branchiae and *O. margoi* has only five. The former species ranges in length from 3.5 to 11 mm, and the latter is 4 to 30 mm (Sawyer et al. 1975; Davies 1978; Lauckner 1985). Both species attach to soft skin surfaces of the axial and inguinal regions, as well as the neck, eyes and cloaca. In heavily parasitized turtles, yellowish mats of leech egg cases are commonly found cemented to the plastron and ventral surfaces of the neck and flippers.

Increasing numbers of green turtles afflicted with debilitating fibropapillomas (fibrous epithelial growths) have been recorded during recent years in the Hawaiian Islands (Balazs 1986; Dailey and Balazs 1987). A concomitant increase in parasitization by *Ozobranchus* has also been seen, especially on the turtles diseased with tumors. Fibropapillomas are highly vascularized, thereby affording ideal sites for leeches to attach. The relationship between *Ozobranchus* and fibropapillomas was first described by Nigrelli and Smith (1943).

Experimental prophylaxes on captive sea turtles parasitized by *Ozobranchus* have included the use of various toxic agents. Schwartz (1974) immersed captive loggerheads, *Caretta caretta*, and green turtles in copper sulfate solution; this treatment proved effective in eliminating *O. margoi* adults and their egg cases but induced increased swimming activity in the turtles. Concentrated topical iodine used by Schwartz (1974) was only temporarily effective. Davies and Chapman (1974) reported that 3 of 85 captive sea turtles heavily parasitized by *O. branchiatus* and *O. margoi* died several months after treatment with copper sulfate, but cause of death was not determined. They also applied 10% formalin directly to the leeches and their eggs, after which the turtles were left out of the water for 3 hours. This treatment, however, was not highly effective (Davies and Chapman 1974). At Sea Life Park in Hawaii, several topical treatments with isopropyl alcohol successfully eradicated *O. margoi* in a massive outbreak on captive green turtles, loggerheads and hawksbills, *Eretmochelys imbricata* (Sea Life Park unpublished data, 1978).

As with any toxic chemical treatment for parasites, there is the possibility of undesirable, acute or chronic side effects to the host. Consequently, the use of a benign therapy would be preferable, if such a treatment were available. On 9 August 1987, a lethargic juvenile green turtle, afflicted with tumors and measuring 55 cm in carapace length, was found stranded at Kailua Beach on the island of Oahu, Hawaii. Numerous *O. branchiatus* were present on the turtle, especially on the ulcerated tumors protruding from the neck and eyes. Egg cases also were present in abundance. The turtle was subsequently held in a shaded seawater tank measuring 2.4 m in diameter and filled to a depth of 0.5 m. The turtle continued to survive in this holding facility, where it was fed chopped fish and squid on a daily basis. Incidental observations made during routine tank cleaning over the following weeks revealed that the leeches seemed to be negatively affected by rinsing with fresh water from a hose. As a result, systematic treatment and observations were conducted. Treatment consisted of draining the turtle's tank completely and filling it with fresh water. When treatment began on 23 September 1987, 120 leeches were attached to the turtle. The leeches reacted immediately to immersion in fresh water by rapidly crawling over the surface of the turtle. Within 30 minutes of soaking in fresh water, leeches began to fall off and were found dead on the tank bottom. After 90 minutes, 80 leeches remained on the turtle. The tank was then drained and refilled with seawater. The number of leeches on the turtle decreased progressively after the freshwater immersion. On the following day, only 35 of the initial 120 leeches remained. Only four leeches remained after 4 days; no leeches were present on Day 6.

Two weeks after treatment, leeches began to reappear, and the egg cases had changed from a dark to a light color. Close examination revealed that the lighter color represented newly hatched eggs. Consequently, it was concluded that the freshwater treatment had little or no effect on the egg cases and that additional treatments would be needed to completely rid the turtle of leeches as new ones hatched. Subsequent immersions were conducted on this turtle and on a second one also found stranded with a heavy infestation of *O. branchiatus*. Eventually, both turtles were completely freed of leeches, and no negative effects were seen.

The relative scarcity of *Ozobranchus* on healthy green turtles in Hawaii suggests that some natural mechanism exists to deter or eliminate these parasites. Hawaiian green turtles commonly use algal and sea grass foraging habitats, where freshwater discharges into the sea. Reduced salinities at these locations may aid in the control of *Ozobranchus* through hypotonic shock. According to Sawyer et al. (1975), both *O. branchiatus* and *O. margoi* occur exclusively in salinities over 30%. Another possibility in controlling leeches is that healthy turtles subject themselves to more frequent grooming by certain fishes at discrete underwater cleaning stations known to exist in Hawaii (Balazs 1980; Balazs et al. 1987). The special circumstance of adult green turtles sometimes basking ashore in Hawaii may also facilitate leech control through heating and desiccation (Whittow and Balazs 1982).

Future research should examine different levels of salinity and duration of immersion needed to effect mortality in leeches on captive turtles. These data may then be used to help explain, or predict, the natural means of parasite control by sea turtles in the wild and to refine a practical nonchemical treatment against leeches in captive turtles.

LITERATURE CITED

Balazs, G.H. 1980. Synopsis of biological data on the green turtle in the Hawaiian Islands. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-7, 141 pp.

Balazs, G.H. 1986. Fibropapillomas in Hawaiian green turtles. Mar. Turtle Newsl. 39:1-3.

Balazs, G.H., R.G. Forsyth, and A.K.H. Kam. 1987. Preliminary assessment of habitat utilization by Hawaiian green turtles in their resident foraging pastures. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-71, 107 pp.

Dailey, M. and G.H. Balazs. 1987. Digenetic trematodes as possible etiologic agent for fibropapillomas in Hawaiian green turtles (*Chelonia mydas*). Proceedings of the 18th Annual Conference of the International Association for Aquatic Animal Medicine, Monterey, CA, pp. 46-50.

Davies, R.W. 1978. The morphology of *Ozobranchus margoi* (Apathy) (Hirudinoidea), a parasite of marine turtles. J. Parasit. 64:1092-1096.

Davies, R.W. and C.G. Chapman. 1974. First record from North America of the piscicolid leech, *Ozobranchus margoi*, a parasite of marine turtles. J. Fish. Res. Board Can. 31:104-106.

Hirth, H.F. 1971. Synopsis of biological data on the green turtle *Chelonia mydas* (Linnaeus) 1758. FAO Fish. Synop. 85, 1:1-8:19.

Lauckner, G. 1985. Diseases of reptilia. *In:* O. Kinne (editor), Diseases of marine animals, pp. 553-626, vol. 4, part 2. Biologische Anstalt Helgoland, Hamburg, 884 p.

Nigrelli, R.F. and G.M. Smith. 1943. The occurrence of leeches, *Ozobranchus branchiatus* (Menzies), on fibro-epithelial tumors of marine turtles, *Chelonia mydas* (Linnaeus). Zoologica, N.Y. 28:107-108.

Sawyer, R.T., A.R. Lawyer, and R.M. Overstreet. 1975. Marine leeches of the eastern United States and the Gulf of Mexico with a key to the species. J. Nat. Hist. 9:633-667.

Schwartz, F.J. 1974. The marine leech *Ozobranchus margoi* (Hirudinea: Pisciolidae), epizootic on *Chelonia* and *Caretta* sea turtles from North Carolina. J. Parasit. 60:889-890.

Whittow, G.C., and G.H. Balazs. 1982. Basking behavior of the Hawaiian green turtle (*Chelonia mydas*). Pac. Sci. 36:129-139.

BARRY K. CHOY and
GEORGE H. BALAZS
Southwest Fisheries Center
Honolulu Laboratory
National Marine Fisheries Service, NOAA
2570 Dole Street
Honolulu, HI 96822-2396, USA
and
MURRAY DAILEY
Biology Department
California State University
1250 Bellflower Blvd.
Long Beach, CA 90840, USA

8917

Chapter 14

The Markets for Chilled Pacific Island Fish in Japan, Hawaii, Australia and New Zealand.

J. Crossland (Japan, New Zealand and Overview)
S. Pooley and K. Kawamoto (Hawaii),
P.W. Philipson (Hawaiian case study) and M.J. Riepen (Australia).

The fishes of the outer reef slope which are the main subject of this chapter have several important advantages over shallow water species for developing an export market. There is a much smaller number of species in deep water than reef and lagoon areas. Several of these species are individually abundant and can be caught consistently which will make marketing easier. Also, deep water species are free from ciguatera fish poisoning. The four main markets in the region for these fish are considered in this chapter.

OVERVIEW

Resources

Traditional fisheries in the Pacific have concentrated on reef and lagoon areas. A wide range of species is taken using a variety of fishing gears including lines, nets and spears. Much of the catch is by subsistence fishermen but in some places such as Fiji a significant commercial fishery has developed. In a few islands lagoons have become heavily exploited and in some cases overfished.

Fishing is also carried on outside the reef. Because of the almost complete absence of a continental shelf around tropical Pacific islands the demersal fish stocks of the outer reef slope are not large. However, there is a small but significant resource of deep bottom fish around most islands. The development of the deep bottom fishery owes much to the work of the South Pacific Commission (SPC) through its Outer Reef Artisanal Fisheries Project (1974-77) and its successor, the Deep Sea Fisheries Development Project, which began in 1978 and is still continuing. A review of these projects for the period 1974-80 is given in Crossland and Granperrin (1980). In addition a large number of country reports on visits by the Deep Sea Fisheries Development Project have been published and these contain important base line data on catches of bottom fish at many places in the region.

The Species

The most important species of the outer reef slope are the deep water snappers. Some authors include all species in the family *Lutjanidae*, others consider the *etelids* to comprise a separate family, *Etelidae*. The etelids are found in deeper water than the lutjanids and make up the largest part of the catches of deep bottom fish. Second to the snappers in importance are groupers of the family *Serranidae*. A large number of species are caught but only a few of these are taken regularly. Other important families comprise the *Lethrinidae, Pentapodidae, Carangidae* and a variety of small sharks.

The most commonly occurring species of the outer reef slope are listed in Table 14.1. A more detailed listing of deep bottom fishes is given in Brouard and Grandperrin (1985).

Resource Assessment

Estimating resource size of fish populations is a difficult procedure. In the tropical Pacific it is particularly so because of the large number of small islands, multiplicity of species compared to temperate regions and a small research capacity. Despite these difficulties progress has been achieved over recent years and several estimates of yields for deep bottom fisheries have been made.

Much of the research has been carried out in Hawaii by the National Marine Fisheries Service (NMFS) and in Vanuatu by the Office de la Recherche Scientifique et Technique d'Outre Mer (ORSTOM). NMFS scientists developed a method of resource assessment based on production per nautical miles of the 100 fathom isobath. A yield of 272 kg per nautical mile was calculated and when multiplied by the total length of the 100 fathoms line a maximum sustainable yield for the fishery was determined. Brouard and Grandperrin (1983) modified this method and applied it to the situation in Vanuatu.

If this method is generally applicable it would provide a quick way to assess deep bottom resources in different places. However, too much

TABLE 14.1
Common bottom fishes of the outer reef slope

Scientific name	*English name*	*Japanese name*
ETELIDAE		
Aphareus rutilans	small-tooth jobfish	*oguchi ishichibiki*
Aprio virescens	green jobfish	*aochibiki*
Etelis carbunculus	short-tailed red snapper	*hachijo akamutsu*
E. coruscans	long-tailed red snapper	*hamadai*
E. radiosus	long-jawed red snapper	*okuchi hamadai*
P. auricilla	yellow-tailed jobfish	*kimadara himedai*
P. filamentosus	rosy jobfish	*ohime*
P. flavipinnis	yellow jobfish	*kinmehimedai*
P multidens	large-scaled jobfish	*nagasaki fuedai*
Tropidinius amoenus	large-eyed flower snapper	*hana fuedai*
T. Zonatus	banded flower snapper	*shimachibiki*
LUTJANIDAE		
Lipocheilus carnolabru	fleshy-lipped snapper	*kibire fuedai*
Lutjanus malabaricus	scarlet seaperch	
L. timorensis		
L. gibbus	paddle-tail seaperch	
Paracaesio kusakarii	Kusakar's fusilier	*shima aodai*
P. stonei	Stone's fusilier	*yanbaru shima aodai*
SERRANIDAE		
Epinephelus areolatus	yellow-spotted grouper	*omonhata*
E. chlorostigma	brown-spotted grouper	*hosekihata*
E. hoedti	blue grouper	*tsuchihozeri*
E. magniscuttis	large-scaled grouper	
E. morrhua	brown-striped grouper	*iyagohata*
E. septemfasciatus	seven-banded grouper	*mahata*
LETHRINIDAE		
Lethrinus elongata	long-nosed emperor	*kitsune fuefuki*
L. variegatus	variegated emperor	*hose fuefuki*
PENTAPODIDAE		
Gnathodentex mossambicus	large-eyed bream	
Gymnocranius		*tamameichi*

lethrinoides		
CARANGIDAE		
Seriola rivoliana	amberjack	***kampachi***
SHARKS		
Squalus megalops	shortnose spurdog	

reliance should not be placed on it at this stage as conditions may well vary considerably in different geographical locations, particularly the slope of the outer reef, which will effect the area of habitat available to deep bottom fishes.

Ciguatera

Ciguatera fish poisoning is caused by the microscopic dinoflagellate, *Gambierdiscus toxicus*, which is associated with benthic algae in tropical reef areas. It enters the food chain as small fish feed amongst the coral and in turn are eaten by larger fish and finally by man. Ciguatera is not usually fatal but can cause severe illness. It is a difficult problem to deal with because of its variable incidence. Certain species are more likely to be poisonous than others but they may only sometimes be toxic. Also, the same species may be poisonous in one place and not in another.

Ciguatera is most frequently found in fishes living in shallow water reef areas, particularly in lutjanids and serranids. There are also a certain number of species which are found over a wide depth range and sometimes occur in the upper part of the outer reef slope. Such species include *Lutjanus bohar*, frequently toxic, and *L. argentimculatus*, sometimes toxic. However, the true deep bottom species are known to be free from ciguatera, probably because their food chain is separate from that of the shallower living reef species.

JAPAN

Summary

Japanese buyers indicated the following difficulties in marketing Pacific bottom fishes in Japan:

- unfamiliar species;
- bias against tropical species which are considered inferior;
- small supply;

- poor image of quality control from Pacific countries;
- doubts about freshness

The first two difficulties can to some extent be overcome by marketing the fish in Kyushu where tropical species are better known. The air route linking Guam to Kagoshima or alternatively Guam to Osaka should be considered as entry points to reduce internal transport costs.

Irregular supply is a difficult problem to overcome with fresh fish when it is based on the small fishing fleets of Pacific countries. It is likely to be less of a problem if exports are dircted to Kagoshima or Nagasaki where they can be added to an existing supply of the same species from local suppliers. However, regularity of supply should be an important priority for exporters, particularly if a species is little known in Japan and its price level is to be determined.

The small quantities likely to be available from Pacific countries make it difficult to enter the Tsukiji market. Importers and traders are used to dealing in container loads, 10 t lots or more, and there is little interest in handling consignments of a few hundred kg. Furthermore, the administration and transport costs for small consignments are much greater on a per kg basis than for large consignments. This may mean that the importer's commission rate would have to be more than the 5 per cent generally used.

In the other markets visited traders were used to dealing in small lots and more prepared to buy in the quantities likely to be offered by Pacific exporters.

The last two difficulties can be overcome if fish of good quality is regularly consigned to the markets. It is important that exporters use a brand name which becomes known as representing quality. However, even if quality standards are high, imported fish are unlikely to achieve the same price as local fish of the same species. The buyers know that the fish has had further to travel, is probably older and therefore has a reduced shelf life. For these reasons imported fish are usually discounted. A measure of this discount can be obtained from the trade in chilled sea bream from New Zealand to Japan. Fresh New Zealand fish achieve prices up to Y2,500/kg. Fresh local sea bream fetch up to Y3,300/kg, or 32 per cent more than the imported product.

The most promising potential export lies in the development of a market for Pacific groupers. These species were consistently the highest priced bottom fish in the markets studied in Japan; the demand also exceeded the supply. Factors enhancing their potential are their lower buying cost in most Pacific countries and their availability at times of highest price in Japan (the northern winter).

If the highest quality standards are maintained a market exists for the long-tailed red snapper, *Etelis coruscans*. The margins are likely to be thin on present prices but the fact that Pacific fish are larger than those now caught in Japanese waters may enable a higher than average price to be obtained.

The short-tailed red snapper, *Etelis carbunculus*, is more abundant in the tropical Pacific than E. Coruscans, but does not command the same price. To market this fish profitably would require regular consignments and promotional activities with the aim of raising its price to that of E. coruscans.

The amberjack, *Seriola rivoliana*, is a low priced fish in most Pacific countries but a comparatively high priced one in Japan. If it can be caught in sufficient quantities it would be a species worth sending to markets in Kyushu.

The fusiliers (*Paracaesio* spp.) achieve good prices in most places in Japan but their available quantities would be a limiting factor in developing an export market for them, as they usually comprise only a bycatch in Pacific countries.

The most abundant bottom fishes in the tropical Pacific are the several species of *Pristipomodies*. Unfortunately these do not command a price sufficient to make their export profitable, except possibly from Palau, because of lower air freight costs.

There appears to be little prospect of exports of frozen fish as the cost of production in the Pacific Islands is in most cases greater than potential returns.

Fish market studies were carried out in Tokyo, other parts of Honshu and in Kyushu. Several species of Pacific bottom fish are known and sold in Japan. The most promising market appears to be Kagoshima where the largest quantities of these fish are handled. A list of preferred species was prepared and costs estimated for getting fish from different Pacific countries on to the Japanese market. Calculations of the prices required to make the trade profitable were made, and showed that for several species the required price level was currently being achieved in Japan.

The Japanese Market

Market structure. Japan's total fish catch is at present around 11 million t annually. In addition it imports a further 1.2 million t and is the world's largest importer of fisheries products. In 1982 imports were worth US$4,000 million.

The fish marketing structure in Japan is very complex, made up of many steps in a long chain, with many inter-connections. A detailed description of the marketing and distribution system is given in the report by Ashenden and Associates (1979) to the New Zealand Government.

Fresh fish entering the Tokyo market (Tsukiji) is likely to pass through the following marketing flow: supplier; importer; primary wholesaler (auctioneer); sub-wholesaler (market place dealer); retailer, restaurant or institution; consumer. In Tsukiji market there are seven companies permitted to operate as primary wholesalers, about 1,200 sub-wholesalers, and 300 authorised large buyers who can also buy at auction from the primary wholesalers. The large buyers may have a different product flow. Some fish purchased at auction may be distributed to markets in other parts of Japan where it may again enter the marketing chain at the primary wholesale level.

J Crossland

Figure 14.1 Deep bottom snappers on sale at Tsukiji market, Japan

Most other large cities and many smaller ones have fish markets. At landing places fish is sold by primary wholesalers on a commission basis for the fishing company or individual fisherman. The number of wholesalers and commission charges (usually 5 to 5.5 per cent) are controlled by regulations. Auction sales may vary from boatloads of frozen fish to boxes of fresh fish to individual fish. After auction the market flow is similar to that described above for Tsukiji. Direct selling by fishermen to their own outlets does not appear to occur at all.

The complex market structure in Japan results from the vast quantity of fish to be sold and the huge numbers of species and types of products. To enable the physical distribution on this scale requires a careful interlocking of the marketing flow. The end purpose of this system is to enable the individual Japanese housewife or restaurant patron to obtain their requirements on a daily basis from the approximately 60,000 fish retail outlets or hundreds of thousands of sushi bars and restaurants.

Chilled fish market. Very high prices can be obtained for the best quality chilled fish in Japan. Apart from live fish, chilled fish obtains the best price for whole fish. However, the highest prices are only obtainable (Y3,000 to 4,000/kg) if the fish is a species suitable for raw fish eating (sashimi). The fish must also be of the freshest quality. Fish not meeting these criteria will command a much lower price, similar to that for frozen fish.

There are many species of Pacific bottom fishes which are suitable for sashimi and it is this sector of the market which should be aimed for in exports of chilled fish to Japan.

Frozen fish market. Frozen bottom fish supplies much of the product for cooked fish dishes at the restaurant, institutional and consumer level. It obtains a much lower price than chilled fish, with an average purchase cost of 350 Y/kg for headed and gutted fish.

Frozen fish is largely sold at fixed price, usually in large quantities (10 t lots upwards). The larger quantities required and lower prices achieved make it unlikely that Pacific exporters could enter this market.

There is a specialised sector of the frozen fish market where higher prices can be obtained. This is for fish frozen in the round to -40° or -45° Celcius. If correctly handled and quickly frozen, such fish can be thawed before sale and used for sashimi or sushi (raw fish on rice). It may obtain a price close to that for chilled fish. However, suitable vessels with the required freezing equipment and onshore cold storage at low temperatures are not available at present in Pacific countries, except in Palau.

Regional factors. The Japanese archipelago comprises four main islands and numerous small ones. It stretches over 3,000 km from north to south and lies between latitudes 24° to 45° N. At least 3,200 species of fish have been reported within 200 nautical miles of Japan (Masuda et al. 1984).

With such a range of latitudes and diversity of species it is natural that distinct regional preferences have developed. The value of a fish may be much greater in an area where it is known compared to an area where it is little seen. Knowledge of these factors is important in selecting the best markets for the sale of particular species. For Pacific bottom fishes the areas where they are best known are Kyushu and the Ryuku Islands.

Seasonal factors. In Japan different species of fish are considered to have a season when they are in the best condition for eating. This is known as the "shun" season. Prices are highest at this time for the particular species. It is unlikely that this factor would affect the fish to be sent from the Pacific.

Other factors such as the seasons for weddings (autumn, spring) or New Year, cause an increase in price for prime species used on such occasions. The demand for groupers is highest towards the end of the year and in the winter. For snappers, which are used as substitutes for sea bream *(tai)*, the highest demand is in spring and autumn.

Species familiarity. An important factor in determining the market price for a fish is its familiarity to the buyer. Fish which are well known will normally realise a higher price than ones which are little or not known. This will hold even if the instrinsic product quality of the unfamiliar species is better than the known species.

Species which are similar to popular Japanese species are easier to sell, even if they are not identical. An example of this is the major trade which has developed in recent years in chilled snapper from New Zealand. the New Zealand species (*Chrysophrys auratus)* is actually a sea bream and closely resembles the Japanese madai *(Pagrus major)*.

It may be possible to market Pacific bottom fishes in a similar way, although even where the same species occur in Japan, they are not well known outside the southern areas.

Field Studies in Japan

Field work was carried out in Japan over the period 26 September to 11 October 1985. During this time discussions were held with government officials, importers, trading companies and fishing companies. Visits were made to markets in Tokyo, other parts of Honshu and Kyushu. The quantities of bottom fish available at the markets during the study was greatly reduced owing to a typhoon passing from the Ryuku Islands to the north of Kyushu between 3 and 6 October. A public holiday on 10 October further reduced the opportunities for market inspection.

Tokyo — Tsukiji

Several species of bottom fish available for export from the Pacific Islands are caught in Japanese waters and sold on the Tsukiji market, but they are seen only in small quantities. Because of their small volume these species are not separately identified in the market statistics and information on throughput and prices are not directly available. Total daily sales at Tsukiji average 2,500 t.

The following view is based on information supplied by traders and wholesalers and from market observations. Prices quoted are for chilled whole fish.

Etelis coruscans. This species is better known as *onaga* than by its proper Japanese name of *hamadai*. It is seen from almost every day to every 2 to 3 days according to different informants. Quantities are small, usually a few (10 kg) boxes a time with around 50 boxes a week offered for sale.

Supply is from Hachijo (Izu Islands) and sometimes from Kyushu. The preferred size is 2 to 7 kg, but many fish are less than this size.

During the market visit on 2 October one 10 kg box containing 5 fish was seen awaiting auction. Inspection of the sub-wholesalers' displays showed the species on sale at four stalls.

Upon capture the fish are not spiked, but placed immediately in an ice slurry which kills them. The quality of fish seen which had been handled in this way was excellent.

The auction price range quoted was Y1,400 to 1,800/kg with better prices being obtained for larger fish. Observed prices at the sub-wholesaler level were Y2,000 to 3,000/kg. The reported usual mark-up between primary wholesaler (auction) and sub-wholesaler is 10 per cent but may be as much as 50 per cent.

Etelis carbunculus. This species takes its Japanese name, *hachijo akamutsu*, from its resemblance to a better known species *Doerderlinia berycoides* (akamutsu). The name indicates it is found around Hachijo Island. It is much less well known at Tsukiji than E. coruscans, and because of this obtains a lower price. The anticipated market price is Y1,000 to 1,500/kg.

Etelis radiosus. Three specimens of this species 5 to 7 kg in size were on sale at a sub-wholesaler for Y3,000/kg. This species is the least common of the three Etelis species and no information on its availability was obtainable.

Pristipomoides siebodi. This is the only one of the six species c Pristipomoides which was observed at Tsukiji and the only one whic appears to be available in commercial quantities in Japan. The estimate price for imported species is Y1,000/kg.

One box of P. sieboldi was observed at a sub-wholesaler at a price of

Y2,400/kg.

Paracaesio caeruleus. This species was more common than any of the preceding ones. It is caught by line in southern Japan and seen regularly on the market. Auction prices are estimated to be in the range Y1,500 to 2,000/kg. Observed sub-wholesaler prices varied from Y2,000 to 2,800/kg. The size range was 1 to 2 kg.

Epinephelus spp. Groupers are rarely seen at Tsukiji. When available they are reported to fetch Y3,000 to 4,000/kg. The preferred size range is 3 to 5 kg.

Kagoshima

Kagoshima in Kyushu is the most southerly of the major cities of Japan. Because of its location, tropical and sub-tropical bottom fish species are important components of its fish market throughput. The quantities handled are large enough to be recorded separately in market statistics. Quantities and prices for species relevant to this study are given below.

TABLE 14.2

Quantities and average prices for selected bottom fish at Kagoshima wholesale fish market, 1983-84.

	1983		1984	
Species	t	Y/kg	t	Y/kg
Seriola rivoliana	118	1,454	151	1,454
Etelis coruscans	217	1,687	185	1,759
Pristipomoides spp	528	1,395	411	1,484
Groupers	123	1,887	115	1,975
Total bottom fish*	2,878	1,094	2,965	1,064

* Includes other species.

There are 44 wholesalers which buy at auction and have stalls within the market. There are approximately a further 100 buyers who can buy at auction but must resell outside the market. Total volume at the market is declining as a lot of tuna is now unloaded elsewhere. Quantities handled average 131 t per day with highest daily sales of 250 t and lowest of 50 t. Kagoshima market is the eighth largest in Japan.

The Kagoshima market was attended on 4 October. Because of bad weather it was a very small market (about 80 t) and the quantities of bottom fish available were about one third of the usual amount. Nevertheless a large number of species common to both the Pacific Islands and Japan were observed. Many of the local names were different from the standard Japanese names given in Table 14.1 These local names are given in brackets in the summary below.

Etelis coruscans (chibiki) — 10 boxes seen, very small fish (0.5 kg or less).
Seriola rivoliana (aka bara) — a few large specimens (up to 10 kg)
Groupers (ara) — small quantities of several species were on sale including *Epinephelus morrhua, E. septemfasciatus, E. maculatus, Variola louti, Cephalopholis miniatus.*

Other species observed were Pristipomoides sieboldi *(inago), Tropidiius amoenus, Erythrocles schlegeli (akabo), Aprio virescens (aomatsu), Lethrinus elongata (kuchime), Gymnocranius spp (tabame),* goatfish *(umigoi)* and surgeonfish. A single specimen of Lutjanus bohar, frequently ciguatoxic in the tropical Pacific, was also on sale. Many of the larger bottom fish particularly groupers, were marked with their weights and sold individually, as large tuna are auctioned in other markets.

After attending the auction, discussions were held with the manager of the bottom fish section of the market. He provided estimates of prices for several species not recorded separately in the statistics. These were in yen/kg:

Pristipomoides filamentosus (kuromatusu)	1,000-1,500
P. multidens	300
P. flavipinnis	600
Tropidinius amoenus	500
Lethrinus variegatus	600
Lutjanus malabaricus	800
Paracaesio stonei	2,000 (if top quality)

The company operating the market is keen to see throughput increased and is willing to receive samples from the Pacific. It is suggested that the following species would be suitable: *Etelis coruscans, Pristipomoides filamentosus, Paracaesio* spp., groupers. The contact for samples is: Mr Kazuma Higo, Managing Director, Taiyo Marine, 34 Jonan-Cho, Kagoshima-shi.

Nagasaki

Nagasaki has a larger fish market than Kagoshima with an average daily throughput of 500 to 600 t. It is an important landing port for marlins caught by gill netters and for trawl fish from the East China sea. The bottom fish species of interest to this study form only a minor part of the catch. The number of boats fishing for deep bottom species is decreasing because of overexploitation of the stocks. Vessels fishing for tropical species used to travel as far as Indonesia and Australia. Voyages were one month with the catch brought back super chilled. Since the introduction of 200 miles zones this fishery has declined but vessels still land in Nagasaki from fishing grounds as far south as the southern Ryuku Islands.

The fish market at Nagasaki was attended on 5 October. On the same day a typhoon was due over the city and as a result most fishing boats were in port and the market was small. The following species with their local names indicated, were seen at the auction: *Seriola rivoliana* (neri, aka bara) — 2 boxes of small fish, one 20 kg specimen; *Gymnocranius lethrinoides* (hidarimaki) — several boxes; *Lethrinus nebulosus* — 1 specimen about 4 kg; *Epinephelus maculatus* — 1 specimen; a few other groupers.

Statistics on landings and prices for these species were not available. The following is a summary of expected prices and availability obtained from the director of the company managing the market, and from discussions with sub-wholesalers.

Etelis coruscans (onaga) — a few only are sold on the market with 30 pieces the maximum in one day. Price not specified.

Paracaesio caeruleus — reasonably common with prices from Y1, 000/kg upwards.

Seriola rivoliana — commonly seen, but in small quantities; 2-3 kg is the preferred size with prices in the range Y1,500 to 1,800/kg.

Groupers — these are usually in short supply and expensive in winter when they fetch Y2,000/kg upwards.

Lethrinus spp and Gymnocranius spp — these are frequently seen in small quantities and fetch Y1,000 to 2,000/kg.

Sharks — many large sharks are landed as a bycatch from the gill net fishery for marlin. In the whole, gutted form they sell for around Y7,000/piece, for fish 80 kg and upwards.

Yaizu

Yaizu is an important landing port for Japan's distant water tuna fleet. It also has a small market for the sale of coastal fishes. However, the main purpose of the visit to Yaizu was for discussions with a company which had been involved with the marketing of tropical bottom fish.

Ishihara Suisan Company carried out trial fishing off north-western Australia over the period 1980-82. Using a 2,000 t trawler and fishing in depths of 120-150 m significant quantities of deep water snappers, groupers and other species were caught. The fish were frozen whole (except for a few large species which were headed and gutted). Freezing and holding temperatures were -40° to -45° C.

The main species caught, and their market acceptability were as follows:

Pristipomoides filamentosus	*average*
P. multidens	*low*
Aphareus rutilans	*low*
Gnathodentex mossambicus	*average*
Gymnocranius robinsoni	*good*
Paracaesio caeruleus	*good*
P. stonei	*good*
Seriola rivoliana	*low*
Caranx papuensis	*low*
Lutjanus sebae	*low*
Epinephelus areolatus	*good*
E. morrhua	*good*
E. chlorostigma	*good*

The company found it difficult to market the fish because of their unfamiliarity. The reported prices achieved for frozen Pristipomoides spp was Y500/kg and for groupers Y600 to 700/kg.

Although the company is no longer dealing in these fishes it has been asked by some of its former buyers for product. The company would be prepared to accept samples and act as a trading house for the sale of bottom fish. An importing company would also be required to handle customs and quarantine clearance. Purchase of chilled fish would be on a commission basis but a fixed price could be negotiated for frozen groupers. As this company is fully familiar with many of the species available from the Pacific Islands it has many advantages over a company to whom the species are unknown. The contact for this company is: Mr Tetsuya Ishikawa, Team Leader, Fisheries Division, Ishihara Suisan Co. Ltd, 1234 Yagusu, Yaizu City, Shizuoka Prefecture.

Shimoda

Shimoda is a small port at the south of the Izu peninsula. A major long line fishery (6,000 to 7,000 t/year) for alfonsino (*Beryx splendens*) is based in Shimoda. Line fishing boats which fish the Izu Islands and the

Ogasawara Islands also unload at Shimoda. These vessels catch Etelis coruscans and E. carbunculus amongst other species. Etelis carbunculus is much less common than E. coruscans.

Retail prices for Etelis coruscans were reported Y3,000 to 4,000/kg and for E. carbunculus Y3,000/kg. At this time of the year prices are high.

Fishing trips for Etelis spp around Hachijo Island last 5 to 14 days, with fish killed by immersion in an ice slurry and then packed in flake ice. With shorter fishing trips common in the Pacific Islands (1 to 2 days) there is no reason why Pacific fish could not be on the Japanese market in as short or shorter time than fish from the southern islands of Japan.

Okinawa

It was not possible to visit Okinawa during the study but some information is available on the types of fish and prices from that area. The principal fishery is for Etelis coruscans and about 500 t per year is landed. The resource is reported to be depleted and only small fish are now caught. Significant quantities of other tropical bottom fish are also landed. Prices of fresh chilled fish are reported in the range Y1,000 to 3,0000/kg with E. coruscans fetching Y1,500 to 2,000 kg. High prices are paid for groupers, particularly red coloured ones. Some Etelis from around the Ryuku Islands is landed in Nagasaki and at times airfreighted there for onward distribution.

Summary of Japan field study phase

Preferred species

Based on the results of the market survey the following ranking of species is suggested:

Groupers (red) most preferred
Groupers (others)
Etelis coruscans
Paracaesio caeruleus
Seriola rivoliana
Pristipomoides sieboldi
Gymnocranius lethrinoides
Etelis carbunculus
Pristipomoides filamentosus
Lethrinus spp.
Pristipomoides flavipinnis
P. multidens
Aphareus rutilans

Tropidnius amoenus
Lutjanus malabaricus least preferred

Prices

Auction prices for the five most common types of deep bottom fish are summarised in Table 14.3. Only the figures from Kagoshima are based on official statistics, the others are estimates from traders.

TABLE 14.3

Auction prices in yen/kg for deep bottom fish at different markets in Japan.*

	Tsukiji	Kagoshima	Nagasaki	Okinawa
Etelis coruscans	1,400-1,800	1,687	1,500-2,000	
Pristipomoides spp.	1,000	1,112		
Paracaesio spp.		1,395	1,000+	
Groupers		1,889	2,000+	3,000
Seriola rivoliana	1,000-1,500	1,454	1,500-2,000	

* whole chilled fish

Handling and packaging

Japan is the most sophisticated and quality conscious market for seafoods in the world. To achieve good prices in this market the highest standards of fish handling and packaging are essential.

Government regulations

Import quotas affect certain species of fish on the Japanese markets. These quotas are for the protection of the Japanese small-scale fishermen. The species affected by quotas are not those which will be potential exports from the Pacific. However, it should be noted that amberjack, *Seriola rivoliana*, is closely related to the yellowtail, *Seriola quinqueradiata*, which is a quota species. Provided consignments of amberjack are correctly labelled with scientific and Japanese name *(kampachi)* confusion should be avoided.

Import tariffs are applied to various fish species imported into Japan. The sample of Pacific fish imported during this study was subject to a 5 per cent duty. The import system provides for a preferential status in which case no duty is payable.

It is the responsibility of the importer to clear quarantine. Although Japan has a recommended maximum mercury level for fish of 0.4 ppm, problems with this regulation are not anticipated.

HAWAII

Summary

Hawaii has become a significant outlet for Pacific Islands fish. In 1987 fresh fish imports were recorded in Hawaii for the following Pacific Island countries: Federated States of Micronesia, Fiji, Kiribati, Marshall Islands, Palau, Tonga and Vanuatu and totalled 170 tonnes. Imports now account for 20 percent of the Hawaiian bottom fish market, and 80 per cent of these imports are sourced from the tropical Pacific.

Demand in the Hawaiian market has continued strongly for some years and, in light of current evolutions in the State fishery, the market is likely to remain in an under-supply situation in the short-term, at least. A number of factors, including attractive prices, availability of airshipment space, species familiarity, high per capita seafood consumption (twice the mainland level) and a relatively less extreme attitude to freshness (compared to Japan, for example) combine to make Hawaii by far the most attractive market for fresh Pacific Islands fish.

Introduction

The remainder of this section (except the case study) is drawn directly from "Status of Hawaii's Bottom Fishery in 1987" (Pooley, S.G. & Kawamoto, K.E. 1988). The consent of the Director, Honolulu Laboratory, NMFS, in allowing the incorporation of this excerpt is gratefully acknowledged.

Recent Developments

The Hawaii deep-sea handline fishery for snappers, groupers, and jacks continued to grow in 1987 although the growth rate apparently levelled off. The fresh fish market for bottom fish remained extremely strong, but because of limited supply, export of bottom fish did not match the growth in the tuna export market. Imports of bottom fish to Hawaii also were high in 1987. Many of these fish were purchased by local wholesalers directly from foreign countries and often exported to the mainland in United States without going through the usual Honolulu market channels.

Although the recorded number of "active"vessels in the Northwestern Hawaiian Islands (NWHI) bottom fish fishery continued to grow in 1987 (from 24 vessels in 1986 to 28 in 1987), by the year's end, only 8 vessels were fishing full time for bottom fish. The other vessels that landed NWHI bottom fish were engaged in other fisheries as their primary target. The multifishery fleet, which included tuna longliners and albacore trollers, accounted for 7 of the 20 other vessels. Another seven vessels dropped out of the NWHI bottom fish fishery entirely. Switching to another fishery, primarily lobster trapping accounted for three more vessels. Two vessels continued to target bottom fish on a part time basis, and one vessel sank.

The motivations behind the decrease in the number of full-time vessels in the NWHI bottom fish fishery are diverse, but two of the main reasons appear to be that concentrations of bottom fish are more difficult to locate and other fisheries have become much more lucrative. Although revenue per trip increased in 1987 to $17,500, annual revenue per active vessel declined ($83,600) because most vessels made fewer trips in the bottom fish fishery.

Many of the more successful bottom fishery vessels switched to longline tuna fishing in 1987. Market prices for Hawaii's longline-caught tuna skyrocketed during the last quarter of 1987 as exports to Japan were re-developed. This, combined with good conditions in the established spiny and slipper lobster fishery and the promising developments in the deep sea shrimp fishery, has posed a strong incentive for traditional bottom fish captains to shift some or all of their effort to these alternative fisheries.

Early in 1988, the Council approved a plan for limited entry in the NWHI bottom fishery. The plan is path breaking in a number of ways, but its approval by the National Marine Fisheries Service (NMFS) headquarters is not assured. If implemented, the limited entry plan will provide a moratorium on entry into the fishery until conditions for renewed entry are established and will provide for exit from the fishery for vessels that do not take at least three trips per year. The limited entry plan was strongly supported by the fishing industry when it was initiated in 1984 and 1985. However, during the ensuing years when the character of the fishery changed from a full-time, directed fishery to a mixed or part-time fishery, many in the industry began questioning the relevance of limited entry. On the other hand, fishery managers and many of the scientists involved in research on Hawaii's bottom fish have argued that the limited entry plan is the least intrusive means of protecting the fishery in the context of the limited biological and economic information on the fishery.

Hawaii Bottom Fish Market

The bottom fish fishery in Hawaii is monitored in two ways: through records of the State of Hawaii Division of Aquatic Resources' (HDAR) commercial fishing reports and the NMFS's wholesale market monitoring program (conducted by the Fishery Management Research Program of the Honolulu Laboratory). Both systems have significant limitations. We believe the HDAR data system undercounts landings in Hawaii because of reporting problems, whereas the NMFS monitoring system is limited to a sample of total landings which must be extrapolated. The NMFS data used in this report are scaled to our estimate of total market quantities, based on previous wholesale market research. The scaling factors are confidential because of the limited number of sources from which NMFS's samples are taken. These factors range from one (indicating zero scaling) to two (representing a doubling of our sample).

The NMFS estimates of recent trends for bottom fish sales in Hawaii (Table 14.4) show a significant increase in landings in Hawaii in 1987 and a 12.5 per cent annual growth rate since 1984. All three segments of the Hawaii bottom fish market (landings in the NWHI and the main Hawaiian Islands (MHI) and imports) have grown over the past 4 years, according to our estimates.

The HDAR data on Hawaii landings show a peak in 1986, but the most dramatic growth occurred between 1974 and 1984 (17 per cent annual growth rate). The HDAR data (preliminary monthly reports suggest a decline in Hawaii landings for 1987, whereas the NMFS wholesale market monitoring estimates show an increase. This difference could reflect a number of reporting, adjusting, sampling, and estimating problems which cannot be resolved yet.

Opakapaka and onaga (large snappers) continue to comprise the largest percentage of landings in the NWHI and MHI fisheries, while hapuupuu (sea bass) is another large proportion of the NWHI fishery and uluas (jacks) comprise a secondary proportion of both fisheries (Table 14.5).

The economic value of Hawaii's bottom fish market has grown with landings over the past two years (1987 and 1986), both in terms of gross revenue and average price (Table 14.6). The NWHI segment of the market has shown volume growth over the past four years. The price distribution between NWHI, MHI, and imported fish is shown in Table 14.7, with quality premiums rising for MHI bottom fish. Prices rose by 13 per cent on average. Bottom fish landed from the MHI received 70 per cent more per pound than NWHI bottom fish. Imports, with potentially 20 per cent of the overall market, pose significant price competition to landings in Hawaii, especially for NWHI landings which have a shorter shelf life. The price premiums shown for MHI bottom fish, despite their smaller average size (cf. Ralston and Kawamoto 1988) continue to reward bottom fishing in the MHI.

TABLE 14.4

NMFS estimate of Hawaii bottom fish market volume, by source, 1984-87 (in thousands of pounds)

Year	*Total*	*NWHI*	*MHI*	*Hawaii only*	*Imports*
1984	1,510	661	697	1,358	252
1985	1,913	922	727	1,649	264
1986	2,013	948	746	1,694	319
1987	2,353	1,017	852	1,869	484

Values are reported in pounds, which is the industry standard in Hawaii. One pound equals 0.45 kg.
NWHI = Northeastern Hawaiian Islands; MHI = main Hawaiian Islands.

TABLE 14.5

Species composition of Hawaii bottom fish catch, 1986 and 1987

Species	*1987*	*1986*
Opakapaka	630,800	485,300
Onaga	350,800	371,500
Ehu	97,400	85,800
Hapuupuu	240,400	245,600
Butaguchi (ulua)	222,400	177,600
Other	245,000	256,500
Total	1,786,800	1,622,300

Bottom Fish Imports Into Hawaii

The pattern of bottom fish imports to Hawaii over the past four years is shown in Table 14.8. Imports account for approximately 20 per cent of the Hawaii market. There has been substantial growth (46 per cent per annum growth rate) in total bottom fish imports from 1984 to 1987. Approximately 80 per cent of the imports come from the tropical Pacific, with Fiji and Tonga being major suppliers. The remainder comes from Australia, Japan, New Zealand, and Taiwan and may not represent the same market niche as Hawaii and other tropical Pacific bottom fish. The data do not provide prices; however, if we applied our monitoring

TABLE 14.6

Hawaii bottom fish market revenue, 1986 and 1987
(in million $)

Source	*1987*	*1986*
Northwestern Hawaiian Islands	$2.3	$2.1
Main Hawaiian Islands	3.1	2.3
Hawaii subtotal	5.4	4.4
Imports	1.3	0.8

TABLE 14.7

Price (per pound) distribution by species and product source for the Hawaii bottom fish market, 1986 and 1987

	1986			1987		
	Market	*NWHI*	*MHI*	*Market*	*NWHI*	*MHI*
Opakapaka	$3.41	$3.20	$3.78	$3.56	$3.27	$3.97
Onaga	8.93	3.13	4.39	4.70	3.24	5.12
Ehu	2.56	2.14	3.32	3.17	2.36	3.75
Hapuupuu	1.61	1.56	2.23	1.93	1.87	2.74
Butaguchi (ulua)	1.32	1.07	2.00	1.19	1.16	2.51
Other	2.43	2.39	2.26	2.42	2.11	2.55
Imports	2.38			2.67		
Hawaii only	2.83			3.10		
Total	2.78			3.02		

Market prices include imports (not shown)

TABLE 14.8

Bottom fish imports into Hawaii, 1984-87 (in pounds)

	1984	*1985*	*1986*	*1987*
Groupers	533	6,600	570	3,992
Jacks	1,102	22,301	44,047	9,144
Sea bass	0	169	4,059	11,893
Snappers	150,814	234,609	270,408	446,610
Total	152,449	263,679	319,084	471,640

program's average imported bottom fish price, ignoring species composition and product form, then the 1987 imports would be worth about $1.26 million.

No imports of snappers, groupers, or jacks were recorded from American Samoa, Guam or the Commonwealth of the Northern Mariana Islands in 1987. Landings from American Samoa and Guam were recorded for previous years.

The import figures are derived from the NMFS Market News Service's annual summaries of fishery products imported to Hawaii. The data are compiled by the NMFS Western Pacific Program Office (WPPO) and are from the Food and Drug Administration (FDA) inspection program. These data provide a more complete species breakdown for Hawaii than do U.S. Customs data, but they are incomplete because only lots valued over $1,000 are monitored and because invoices for lots pulled for inspection are not available for WPPO recording. The data cover all sources outside the U.S. Customs area, including American Samoa, Guam, and the Commonwealth of the Northern Mariana Islands. Furthermore, because of a minor sampling problem, annual totals for 1987 needed to be extrapolated. These summaries do not distinguish product form, whether round or fillet. However, in 1987, 94 per cent of the snapper imported into Hawaii was in whole form (this does not include snapper brought to the State from the mainland United States). The data refer only to fresh/frozen imports and not to any processed products. Not all of the imported bottom fish remain in Hawaii; some may be re-exported to the mainland United States by local wholesalers and brokers.

Case Study — Hawaiian Fish Distributors (HFD)

This section describes a case study of the operations of a fish broker operating in Hawaii who buys fish in from various sources and prepares, markets and ships the product to U.S. mainland and Hawaiian buyers. It is typical of the kind of operation that it would be necessary to establish to effectively dispose of marketable surpluses of bottom fish and tunas directly from Pacific island locations.

For reference purposes the following table sets out common Hawaiian names for popular fish.

The processing and shipping operation of HFD is centered on the plant at Kailua-Kona on the island of Hawaii, 45 minutes by air from Honolulu. The principal source of fish is locally based commercial fishermen, but Micronesia has been developed as an additional source of fish, and is particularly useful to augment the number of varieties that HFD is able to offer its customers, particularly in the white fish area.

A graduated scale of payment is used depending on HFD assessment of

TABLE 14.9

Some commonly caught fish in the Hawaiian market, English, Hawaiian, and Scientific Names

English Name	*Hawaiian or local name*	*Scientific Name*
Albacore	Tonbo/Ahipalaha	*Thunnus alalunga*
Amberjack	Kahala	*Seriola dumerilii*
Bonito	Kawakawa	*Euthynnus yaito*
Dolphin Fish	Mahimahi	*Coryphaena hippurus*
Jacks (Trevally)	Ulua/Paio	*Caranx spp.*
Japanese mackerel	Saba	*Scomber japonicus*
Milk Fish	Awa	*Chanos chanos*
Mullet	Ama'ama	*Mugil cephalus*
Omaka	Omaka	*Caranx spp.*
Parrot fish	Uhu	*Family Scaridae*
Red Jobfish	Lehi	*Aphareus rutilans*
Scad, Big-eye	Akule/Aji	*Trachuropscrumenophthalmus*
Scad, Big-eye (young)	Halau Hahalalu	
Scad, Mackerel	Opelu	*Decapterus pinnulatus*
Seabass (Grouper)	Hapu'upu'u	*Epinephelus spp.*
Snapper, red	Ehu/Efu/Ula'ula	*Etelis carbunculus*
Snapper	Gindai/U'hikiki	*Pristipomoides zonatus*
Snapper, pink	Kalikali	*Pristipomoides sieboldi*
Snapper, red	Onaga/Ula'ula	*Etelis coruscans*
Snapper, pink	Opakapaka	*Pristipomoides filamentosus, P. multidens & P. flavipinnis*
Snapper, grey	Uku	*Aprion virescens*
Tuna, big eye	Ahi/Shibi/Menpachi	*Thunnus obesus*
Tuna blue fin	Ahi/Mauguro	*Thunnus orientalis*
Tuna, skipjack	Aku	*Katsuwonus pelamis*
Tuna, yellow fin	Ahi/Yashibi	*Thunnus albacares*
Wahoo	Ono	*Acanthocybium solandri.*

Source: Adapted from Peterson 1976

the quality of the fish being offered; all fish is cored through the belly cavity to assess quality on receipt.

Grade 1 fish is up to Japanese sashimi standard and goes mainly to ethnic Japanese buyers on the US mainland. Tuna of this quality is shipped in headed and gutted form as buyers will not accept loins. About 20 per cent of the fish received is to grade 1 standard, although there are seasonal variations.

Grade 2 fish is still of sashimi quality but not to acceptable Japanese standard. The flesh is of a lighter colour. This fish is all shipped as loins. About 40 per cent of the landings fall into this category and HFD pays only 75 per cent of the grade 1 price.

Grade 3 fish is not suitable for sashimi and is utilised in various cooked tuna dishes. This constitutes the remaining 40 per cent of purchases and only fetches the fisherman 50 per cent of the grade 1 price. This fish is also shipped as loins.

Depending on prices and demand, fish are also bought in from the local auction and other sources within Hawaii, including the Honolulu fish auction. At the time of the preparation of this report several large (25 kg) ehu were being processed into fillets for subsequent sale in Portland and San Francisco. These fish were purchased at the Honolulu market after having been consigned, whole, from Fiji, and flown to the Kona processing operation. HFD uses an agent in Honolulu to make purchases such as this as auction prices allow.

Approximately half the fish purchased is filleted before shipment. Those usually filleted are large bill fish, lower grade tunas, ono and mahi mahi. After removal from the frame, the fillets are washed and placed on absorbent paper to dry, and wrapped in an inner layer of clear cling wrap and an outer layer of butchers paper. Packaging materials consist of a corrugated board outer carton, printed with HFD logo etc. on the outside and coated with wax on the inside. A corrugated board insert is placed in the outer when it is erected to stiffen it. The erected outer is placed over a mould lined with a blue light-weight high-density polythene bag and injected with polyurethane foam. This results in the coating of the entire interior walls and base of the box with approximately 3 cm of insulating foam, faced with the polythene bag. The bag is made oversize so that the top can be folded over as flaps. A single sheet of the same material is made separately to form the insulating interior lid to the container. The completed box measures 100 cm x 40 cm x 40 cm and weighs 5 kg. The completed boxes, while still empty, are kept for 12 to 24 hours in the chill room to assist in fish temperature control.

A second bag of heavy grade low density white polythene is placed inside the box and the fillets, trunks and whole fish placed directly into it. Care is taken to ensure that larger tougher textured fish, such as mahi

mahi, are placed at the bottom. After filling the bag, usually with about 60 kg of fish, the bag is folded closed and five 1 kg single use gel packs are removed from the freezer and placed on top of the bag and the box is strapped shut. Gross weight is in the area of 70 kg. A record is kept of the contents of each box as it is filled and this is written on the outside of each box, and on the air way bill. In the case of fillets, up to eight cardboard internal dividers are used to prevent crushing and shake-down of the product during shipment. This also enables single gel packs to be placed in each compartment, on top of the wrapped fillets.

All top grade sashimi fish are shipped headed and gutted by buyers preference, although HFD is attempting to persuade buyers to accept loins for sashimi fish. Beyond the obvious freight savings, HFD believes that quartering the fish on receipt would allow much quicker chilling and significantly reduce burning. HFD believe sashimi grade fish must be reduced to 3° C or less within four hours of being caught. Headed and gutted tunas are shipped with about eight gel packs in the standard container fitted with a specially moulded base section to hold the trunk in position during shipment. Some fish are shipped whole, particularly smaller bottom fish and sometimes small tunas for display purposes.

In total, shipments from the HFD Kona plant to the US mainland range between 5,000 to 15,000 kg each week. During peak periods up to ten persons are employed falling back to only two or three during slack winter periods. There are three non-stop flights from Kona to San Francisco each day, of which two are United aircraft which are used by HFD. United operates a chill store in San Francisco and is responsible for holding and transhipping on to onwards flights (which are also all United) within the US. On some occasions it is suspected that fish in transit at San Francisco is not being placed in the airport chill store, and HFD is using time/temperature monitors to evaluate this problem. Fish generally takes less than 40 hours to reach the destination airport from Kona; United guarantees delivery to any mainland airport it serves within 48 hours of despatch. HFD is currently shipping fish from Kona to 33 of the mainland States, as far away as New York.

As each box is packed out it is weighed and marked with place in the consignment (e.g. 1 of 3) and has a sticker placed on it showing Air Way Bill (AWB) number, total pieces in shipment, total shipment weight, weight of that piece, destination airport and date. HFD maintains its own series of AWB numbers. A packing slip showing contents is enclosed within the box. HFD transports the packed boxes to the airport on an open flat-bed truck (20 minutes). On arrival they are received by a shipping agent who prepares the AWB and arranges loading, etc. with the airline. A copy of the AWB is attached to the outside of the box. After despatch is confirmed the buyer is contacted by phone and advised of the estimated arrival time and AWB number. When due he will contact the airline, if not already contacted by them, quote the AWB number and take delivery.

All fish is shipped to order; that is pre-sold. Each day, each of the regular buyers on the US mainland (approximately twenty) is contacted by phone and his requirements are obtained. This occurs between 6 am and 7.30 am, Hawaiian time. This is matched against HFD's available inventory, the order agreed, made up and shipped to catch the first flight to San Francisco which departs at 11.40 am that same morning. Any surplus inventory that remains unsold is moved by contacting, by phone, additional potential buyers until all stock is committed. An additional shipment can be made, if necessary, to clear any residual fish on the second flight to San Francisco that departs at 8.15 pm.

All the mainland buyers are fish distributors themselves, who repeat the above placement process with their own outlets.

In order to upgrade the process of pre-selling the fish bought in prior to shipment, which is a key element in avoiding the potential losses of open auction sales, and the serious losses associated with freezing fish, HFD is establishing a sales office on the US mainland which is linked by computer to the Kona processing operation. As fish is received at Kona it is added to a computerised inventory, which is updated as the fish is shipped or otherwise disposed of. This means that the current stock holding of fish at Kona is always held on the computer there. This computer is linked with another at the US mainland sales office, thereby enabling sales staff to have an accurate inventory of stock to be sold. In practice, because of the time differences, selling against this stock occurs during the Hawaiian night, and the HFD Kona operation is able to start up with a listing of pre-sold orders that have been secured and transmitted to them from the mainland office. This has the advantage of minimising the need for phone selling from Kona, and helps to ensure that the maximum shipment is sent on the early flight.

AUSTRALIA

Summary

Pacific Island bottom fish are are a prime quality white flesh table fish species which are in strong demand on the Australian market. The Australian fresh and frozen fish market is heavily reliant on imports to satisfy local demand with total imports steadily rising to be currently exceeding 65,000 t or 55 to 60 per cent of total apparent annual fish consumption. Large increases have been recorded for both imported whole fish and frozen fish fillets.

With improved economic conditions and a firming of meat prices, demand for table fish species like deep water snapper can be expected to increase, and prices for good quality whole fresh chilled and frozen white flesh fillets to remain firm especially on a spot basis when local supplies are low. This usually occurs in the first two months of each year.

An analysis of the various market segments and marketing channels would suggest that regional suppliers would be advised initially to market its fish through the State Fish Auction Markets in Brisbane and Sydney. In addition to displaying and selling product on the State Auction Markets it might also be advisable to conduct a promotion in Sydney. This could be done in association with the South Pacific Trade Commission and be targeted for a small number of selected reputable seafood restaurants to gauge possible buying interest and price levels. A more focused marketing strategy should only be considered after an evaluation of initial sales on the respective State Fish Auction Markets and from feedback received from the restaurant promotion in Sydney.

Review of Australian Import Regulations

Australia has a relatively open tariff policy in respect of fisheries products. The South Pacific Trade and Economic Co-operation Agreement (SPARTECA) does not place the Forum Island Countries in an advantageous tariff position in respect of fisheries exports to Australia, because, in general, all fresh, chilled and frozen fish regardless of its source enters Australia free of import duty.

Quarantine provisions included in the Australian import regulations are relatively strict. Fish exports from the region will not generally be subject to intensive plant or animal quarantine checks, however food quarantine requirements in respect of mercury testing is of possible concern. The Customs (Prohibited Imports) Regulations specify that all fish and fish products for human consumption with a mean mercury content in excess of 0.5 parts per million are prohibited imports. It can be expected that airfreight shipments from the region will generally be small and consist of a number of different species of fresh chilled fish. If all species are to be tested and/or significant delays in delivery are caused (ie. longer than 1 or 2 days) the economic viability of such trade is in serious doubt.

In discussions with the Australian authorities attention was drawn to the possibility of having species tested for mercury, and if appropriate, be added to the exempt list for mercury analysis as specified in Appendix D24 to the Customs orders. As this would avoid the need for mercury testing of each consignment such a procedure should be carrried out prior to commencing exports to Australia.

Importing into Australia, as in most parts of the world, requires documentation. Familiarization with the completion of the appropriate certificates and forms is essential. The commercial invoice and veterinarian or certificate of origin should clearly state the name of the fish including scientific and if possible common Australian marketing name; whether it is perishable, fresh chilled, frozen or otherwise and its processed form, ie. whole, gilled and gutted, or otherwise processed. The presentation of clear and accurate documentation will ensure rapid processing through Customs.

Fish Marketing

In many States of Australia the control and management of traditional fish auction markets are vested with the State. Such auctions account for a majority of local fresh fish sales and very small percentage of imported fisheries product sales. In Brisbane and Sydney the Fish Marketing Board or Authority is responsible for conducting and managing the fish auction markets and also to co-ordinate and promote the orderly marketing and distribution of fish throughout the respective States. The fish markets are self-financing with commission rate being charged depending on type and quantity sold. These range from 5 to 12 per cent.

The State Fish Auction Markets receive fish in many forms from fresh chilled whole fish to frozen cooked crustaceans and may be sourced from either local supplies or imports. However, in general, the vast majority consists of fresh chilled whole or gilled and gutted fish from local fishermen's cooperatives and individual fishermen.

Buyers at the fish auctions comprise a wide variety of intermediate and end-user markets. Typically they consist of fish processors, wholesalers and/or retailers, supermarket chains and restaurant buyers. On the days of visits there were about 40 to 50 buyers in Brisbane and 100 to 150 in Sydney. Bidding for fish was brisk with resulting price depending on a number of factors including species supply and demand, quality demand, quality, size and form.

Deep bottom fish are relatively unknown on the Australian market. Some species on the Brisbane market would most closely resemble the Pacific islands catch, however the similarity is limited to those species caught in relatively shallow waters. Because Pacific bottom fish are handlined from depths exceeding 100 m and as the Australian fishing industry does not generally utilise such fishing methods, such species are not normally landed and sold on the local market. Snapper (*Chrysophrys*) is sold on all three auction markets and provides some understanding of the table-fish market and serves as a useful reference for potential bottom fish sales. Sydney is dominant in the snapper market selling in excess of 600 t per annum. Melbourne is reported to sell in excess of 200 t per annum with Brisbane selling less than 50 t per annum. Reasons for the low snapper sales in Brisbane are the lack of supply and the availability of alternative good quality table fish species like emperor, perch, coral trout and barramundi. Prices for snapper are consistently highest in Sydney with margins typically A$0.50 to A$0.70 per kilogram over Brisbane and Melbourne.

Wholesale Distributors and Importers. Wholesale distributors and importers operate in all States in Australia and tend to deal mainly in frozen and processed fish products. However, some also handle fresh chilled gilled and gutted, headed and gutted, and frozen filleted fish especially for some of the more popular species from New Zealand.

Well established reputable companies in this sphere of business usually not only handle and hold a wide range of seafood products but also extend credit and operate cold storage and possibly processing facilities. As such, product lines must be fast moving and/or have high margins. Typically margins in this sector exceed 20 per cent and often 50 per cent on some of the slower or higher risk lines. The Pacific region could have products which are suitable for such marketing. However, price, unknown frequency of supply, and lack of market experience will severely limit potential interest.

Specialist High Quality Table Fish Marketing. This market sector comprises a number of entrepreneurs who deal direct with the restaurant/catering trade and specialist fish retailers and provide a very limited yet high quality and well presented and packaged product. It is an up-market sector with emphasis on quality presentation and packaging.

This sector would be the desired market for much of the air-freighted Pacific Island fish. While a top quality product can be produced in the region this market cannot be considered until high quality and consistency of supply can be guaranteed. The long term objective for regional trade directed to Australia should however be to target to this market sector.

Import Regulations

General. Imports into Australia are regulated by the Commonwealth Government with the various States administering a uniform set of controls. This applies to all customs and quarantine regulations. Each State does however have its own unique legislation relating to the production and sale of edible products which are generally covered under its health regulations.

Customs Tariff. Australia has a relatively open tariff policy in respect of fisheries products. In general all fish, fresh (live or dead), chilled or frozen, whole or filleted imported into Australia is free of import duty. Processed fish products including canned fish attracts a duty of up to 10 per cent. The South Pacific Trade and Economic Co-operation Agreement (SPARTECA) does not place the South Pacific in an advantageous tariff position in respect of fresh chilled and frozen fisheries imports into Australia.

Quarantine. The Commonwealth Department of Health is responsible for import quarantine control. Quarantine controls cover three distinct fields namely plant, animal and food. Plant and animal quarantine controls are administered by the Department of Agriculture or Primary Industry within each State and with respect of food and foodstuffs the State Department of Health or the Australian Government Analytical Laboratories (AGAL) are responsible for carrying out any testing that may be required.

Fish is generally exempt from plant quarantine excepting if the packaging materials are made of plant matter; or the country of origin has certain specified diseases. Fish exports from the region should meet all plant quarantine requirements.

Animal quarantine prohibits the import of certain fish species and in particular the salmonids including salmon and trout. Most other fish and fish products may in general be imported from any country. Animal quarantine checks will typically only be made on fish if the fish is live or the fish products contain milk or egg as for example batter or fishballs.

Food quarantine provisions included in the Australian Customs regulations refer to maximum levels of additives, metals and other agents that may be present in specified foods and foodstuffs. In respect of fish the important provisions relate to the allowable mercury content. Item 18 of the second schedule of the Customs (Prohibited Imports) Regulation states that all fish and fish products (including crustaceans and molluscs) for human consumption with a mean total mercury content in excess of 0.5 parts per million (ppm) with a maximum individual sample concentration of 1.5ppm are prohibited imports. This level of 0.5 ppm was recommended by the National Health and Medical Research Council (NH & MRC) and is included in their Model Food Legislation Reg. A12.

The request for mercury analysis is initiated by the customs inspector at the point of entry. The frequency of testing depends on a number of factors including the track record of the particular species from the country in question and whether it is exempted from normal testing as specified in Appendix D24 of the Customs Orders. New species from a new source will almost certainly be sampled for mercury. Of note in the testing procedures is the number and type of samples required for mercury analysis which, for small shipments would make such shipments uneconomic if samples were taken.

From discussions with the Customs departments, the various State Health departments and AGAL it is apparent that mercury testing is a procedure which in time takes no longer than one day but which for Queensland may take up to 10 days from the time samples are drawn to results being reported. In N.S.W. and Victoria the corresponding times are one to three days. The difference in times is due to the fact that Queensland only performs mercury testing on a specific weekday whereas the other States do them when and as required.

Health. As stated above, each State is responsible for the legislation and regulation of the production and sale of food and foodstuffs in their respective States. Such regulations cover all goods available for consumption whether imported or locally produced.

Each State (excepting Tasmania and South Australia) has adopted the standards as recommended by the NH & MRC in respect of mercury contents, however, with the production or sale of shark significant differences do occur.

Certificates, forms and Document processing. Importing into Australia requires certain documentation. Regardless of product quality or shelf life the product will not generally be allowed to enter Australia if the appropriate documents, correctly completed, are not submitted. Familiarisation with the correct certificates and forms is essential. The presentation of clear and accurate documents ensures that processing through customs is achieved with maximum speed and efficiency. Typically document processing by customs requires no more than three working days. It is standard with perishable products for the customs clearing agent to request the removal of the goods to a chiller or cold store, and to the market, prior to making the customs entry.

Exporting marketing strategy

Pristipomoides and *Etelis* are prime table fish species and should receive good prices in all markets, especially Brisbane and Sydney. Brisbane is an attractive market as it has a range of tropical species similar to the regional catch. Sydney, however, with its numerous restaurants and relatively high per capita income, has a strong and increasing demand for high quality table fish. The low period in supply also coincides with many regional peak supply periods and in such a period prices paid for good quality white flesh fish are very high, especially for the small table size fish. Medium and large size fish do not tend to attract the same high prices.

Until trial shipments are sold in the respective markets further refinement of a marketing strategy cannot be advised. Although in the long term sales direct to the restaurant trade are desirable it is strongly advised that initial shipments be auctioned at the Queensland and N.S.W fish auction markets. This will enable the product to be displayed and promoted to many restaurant buyers and will assist in the selection of the most appropriate marketing strategy and/or potential buyers.

In collaboration with displaying and selling product on the respective markets it would also be desirable to conduct a promotion in Sydney. This should be done in association with the South Pacific Trade Commission and should target on a small number of selected reputable seafood restaurants to display and test the product and gauge possible buying interest and price levels.

Whether the Australian market will readily purchase the Pristipomoides and Etelis species at prices required to make the trade viable is difficult to assess. On an opportunist basis supplying fish on low supply periods should provide good returns. However, to ensure the successful development of long term year-round trade, fish from the region will need to be consistently well presented and be of the best quality.

NEW ZEALAND

Summary

There would appear to be significant market for Pacific Islands fish in Auckland sufficient to absorb currently available surplus production from the FFA states mentioned in this section. There is also a potential market for tuna and other pelagic fishes, the size of which is not known. Margins are expected to be tight and supply will be influenced by returns elsewhere, principally the USA market. Possible prices which could be achieved selling at the wholesale level (i.e. to retailers direct) are given in Table 14.10. These are estimates only based on prices realised for similar New Zealand species and will have to be tested by actual experience.

The potential for exporting fresh skipjack and yellowfin appears promising. While large yellowfin (30 kg) can fetch high prices in Japan the price for small fish is much less. However, small fish would be the preferred size for sale at the weekend markets in Auckland. If local companies decided to market purse seine caught skipjack within New Zealand in the fresh form this could weaken the market. On the other hand the skipjack season in New Zealand lasts from December to March only, leaving the rest of the year when fresh product would be unavailable, unless imported.

TABLE 14.10

Estimated prices per kg for chilled Pacific Islands fish in the Auckland market (wholesale level).

Species	*Form*	*NZ$*	*FJ$*	*WS$*	*T$*	*SI$*
Snappers	whole	4.00	3.92	5.43	3.65	5.45
Breams	whole	4.00	3.92	5.43	3.65	5.45
Emperors	whole	4.00	3.92	5.43	3.65	5.45
Yellowfish	whole	3.00	2.94	4.07	2.74	4.09
Skipjack	whole	3.00	2.94	4.07	2.74	4.09
Snappers	H&G*	9.00	8.82	12.21	8.21	12.26
Groupers	H&G*	9.00	8.82	12.21	8.21	12.26
Dogfish	Trunked	6.00	5.88	8.14	8.17	5.47

*Wing off ("Wing" refers to the pectoral and ventral fins)
Exchange rates as at Feb 1988.

If exporters from FFA member states wish to develop a trade in fish as a joint venture with a New Zealand partner it may be possible to obtain financial assistance through the Pacific Islands Industrial Development Scheme (PIIDS) which was established in 1976. The scheme's main objective is to foster economic development and the growth of employment in island countries. However, since PIIDS assistance is currently only available for manufacturing processing or pioneer agricultural ventures it is unlikely that purely exporting projects would qualify. Details of PIIDS are available in a booklet which can be obtained by writing to:

The Executive Officer
PIIDS Unit
Department of Trade and Industry
Private Bag
Wellington, New Zealand

Introduction

As indicated in the introduction to this chapter, in recent years an increasing number of Pacific countries have established an export trade in air-freighted fish. The principal market has been the USA (Hawaii) but some fish has gone to Japan. Trade has also developed within the Pacific Islands themselves, such as that from Palau to Guam and the Northern Marianas. This trade has been dependent on good air links, competitive air freight rates and attractive prices in the importing countries. However, not all Pacific countries can take part in it because of the lack of convenient transport or high freight costs.

For some countries, for which exporting to Japan or the USA is difficult, there may be an alternative market in New Zealand. Countries to which this could apply are Fiji, Solomon Islands, Tonga and Western Samoa. Other countries could also be interested provided there are good air connections with New Zealand.

The possibility of exporting frozen fish by sea freight exists, but in most cases this is not a practical alternative. Refrigerated cargo space is available from New Zealand to the islands but shipping companies seldom offer it on the return because of lack of demand.

In the past New Zealand has not been considered a potential market because of its own large fishing industry. However, since the introduction of individual transferable quotas to the catching sector and total allowable catches for most of the main species in October 1986, this situation has changed. There have been severe cuts in the allowable catches for important species on the domestic market (e.g. snapper and grouper). This, plus the competing export market, have resulted in local shortages, particularly in Auckland area, and have forced up prices. At the same time the New Zealand dollar has strengthened against the currencies of the Pacific Islands. There would thus appear to be a market niche which could be supplied by fish from the Pacific Islands.

Marketing niches for Pacific Islands fish

It is likely that marketing opportunities will be primarily for fresh chilled fish. This product is more readily acceptable on the New Zealand domestic market than frozen fish. Most fish in New Zealand is sold fresh. Fresh fish can be sold whole or processed into fillets or steaks before sale. Processing is less satisfactory when carried out on frozen fish, particularly if it has not been blast frozen. However, the export of frozen fish should not be entirely discounted as there may be a market for frozen in the round. Also, larger consignments may be consolidated and advantage taken of cheaper air freight rates.

The principal market is likely to be amongst the ethnic Polynesian population. Large numbers of people originating from Western Samoa, Tonga, Cook Islands, Niue and Tokelau and their descendants live in

New Zealand. The largest number of these are concentrated in the Auckland urban area. Population figures by ethnic origin from the 1986 census showed the following.

TABLE 14.11

Ethnic origin of New Zealand population

	European Origin	*NZ Maori*	*Pacific Is Polynesian Origins*	*Others*	*Total*
New Zealand	2,651,379	404,775	125,850	81,279	3,263,283
Auckland	611,370	91,233	80,822	25,951	809,376

In addition to Pacific Island Polynesians there are numbers of people from Fiji in New Zealand. In total the potential ethnic market in Auckland is larger than any of the urban centres in the Pacific Islands.

People of Pacific Island origin maintain many of the customs of their home countries. Important amongst these are traditional food consumption patterns. Fruit and vegetables from the islands are regularly imported— taro, plantain, banana, coconut, etc. The importance of fish and other seafoods is much greater for Pacific peoples (and New Zealand Maoris) than for the European population of New Zealand. Per capita consumption of fish is considered to be much higher amongst Polynesians than the New Zealand population as a whole, although official figures are not available to confirm this.

Apart from prepared foods (e.g. fish and chips) most of the fish bought by Pacific Islands people is in the whole form. Weekends are traditional buying days in preparation for the family meal on Sunday. Much of the fish for this purpose is bought from the open markets which operate on Saturdays and Sundays at a number of places in greater Auckland. In addition, fish retail shops in suburbs where there is a large Polynesian population sell much of their product in whole form.

Another possible market is to supply premium fish for processing into fillets for sale through retail fish shops. Fish for this purpose could be air freighted in the headed and gutted form. Savings of at least one-third in air freight and packaging costs could be achieved for fish transported in this form.

Suitable species for this market would be deep water snappers and groupers. Both of these have names familiar to consumers in New Zealand where the local snapper is generally considered to be the prime table fish and groper (a spelling variant of grouper) is another highly regarded species. They could therefore be sold under their usual common names (perhaps as Pacific snapper, Pacific groper) without misleading the public or contravening labelling requirements. In fact, the New Zealand snapper is really a sea bream (family Sparidae) whereas the Pacific snappers are true snappers (family Lutjanidae).

A third possible market may exist for speciality products for high class food retailers or seafood restaurants. Because of their visual appeal species such as the long-tailed red snapper could find a market in New Zealand. Another possibility is the sale of high value crustaceans (tropical rock lobsters, slipper lobsters, reef crabs). This market may not be an easy one to develop but because of the value of the product it would be able to support a relatively high level of freight costs.

The New Zealand Domestic Market

Most fish sold at the retail level in New Zealand is processed before sale. Usually this is into skin off boneless fillets. Some larger fish like groper or ling are cut into steaks or blocks. Whole fish are sold also but represent a much smaller proportion than fillets. The amount of whole fish offered for sale depends on the location of the retail outlet. In areas with large Polynesian populations or other ethnic groups used to buying fish in the round it is readily available.

As previously mentioned, sales of fresh fish predominate, particularly through speciality fish shops. However, increasing quantities of frozen fish are now being sold. Much of this comprises deep water species (orange roughy, oreo dories, hoki) which is sometimes frozen at sea. It is usually thawed before sale and sold as "pre-frozen."

Retail fish prices are currently perceived to be high by New Zealand consumers. This is because most fish is sold as boneless fillets. For most species of fish the yield in this form is 25 to 35 per cent of the whole fish weight. Thus a fish valued at NZ$5/kg whole would produce fillets selling for NZ$14.30 to $20.00/kg. Such prices appear high when compared to those for meat. There are therefore barriers to further price increases for fish at present. In fact, per capita fish consumption began to fall in 1985 after a long period of increasing consumption. This is thought to be due to price resistance. Recent consumption rates for fin fish are given in Table 14.12

Two factors have contributed to price increases over the past two years. Firstly, there was the Goods and Services Tax (GST) introduced on 1 October 1986, which added 10 per cent to all prices. All prices in this report include GST unless otherwise mentioned.

TABLE 14.12

New Zealand fin fish consumption 1980-1986

Year	*Per Capita Consumption (kg)*
1980	13.60
1981	13.51
1982	15.56
1983	23.39
1984	26.45
1985	21.60
1986	19.63

Source: N.Z. Fishing Industry Board

Also on 1 October 1986 a new fisheries management regime was enacted. The scheme is based on individual transferable quotas (ITQs) and total allowable catches (TACs) for all the main commercial species. The size of ITQ a fisherman received was determined by his past catches. The sum of ITQs equals the TAC for each species. An important reason for introducing the scheme was the conservation of the resources. Many species of coastal fish had become overfished. When the scheme was introduced the government reduced TACs below previous catch levels for a number of species. This resulted in a shortage of fish on the local market, particularly prime species like snapper and groper which had strong export markets.

Current price information is given in Table 14.13 (whole fish) and Table 14.14 (Fillets). This information was gathered from fish shops in the Auckland central city area, Herne Bay, Ponsonby and Otara.

TABLE 14.13

Retail Prices for whole fish,
Auckland, February 1988 (NZ$/Kg)

	Fish shops			*Otara*	*Avondale*	*Average*
Species	*1*	*2*	*3*	*market*	*market*	
Snapper	6.50	7.50	7.00	6.60-6.80	7.00-7.50	6.98
Golden snapper	6.55	7.50	6.60			6.88
Trevally	3.95*	4.50	3.80	5.00		4.31
Mullet	4.70	4.50	3.80	4.50-500		4.50
Skipjack				6.00		
Paddle crab	5.28	5.00				5.14
*gutted						

TABLE 14.14
Retail prices for fish fillets,
Auckland, February, 1988 (NZ$/Kg)

Species	*Fish shops* 1	2	3	4	*Average*
Snapper	19.50	19.00	19.00	21.00	19.62
Gurnard	12.85		14.85	13.80	13.83
John Dory	19.75*	19.50	19.60		19.62
Tarakihi	15.95	16.60	17.50	16.95	16.75
Trevally		8.20*	8.80*		8.50
Lemon fish	10.74	9.80	10.85	10.45	10.48

*Skin on

The prices for whole fish show that snapper averaged nearly NZ$7.00/kg. This shows an above average mark-up over the reported wholesale price of NZ$4.00 to $4.25/kg.

Although this study was carried out in the middle of the New Zealand skipjack season, only one outlet offered this species for sale and at the high price of NZ$6.00/kg. It appears that skipjack is caught only for the canning market and no attempt is made to market it locally in fresh form. In general, tuna is very seldom available in Auckland, where there would be a large market amongst the island people. The species most commonly seen is albacore; yellowfin is not available at all.

Much of the snapper sold in whole form is of average to poor quality, particularly that sold through market stalls. Top quality snapper goes mainly to the export market. Overall the freshness and quality of whole fish in Auckland is not good. Surprisingly, it appears to return the retailers a higher profit margin that better quality fish processed into fillets.

The fillet prices shown in Table 14.14 are for the commonly available species in Auckland, and those with which imported fish would compete. Highest average prices are for snapper and john dory (NZ$19.62 for both) and lowest for trevally (NZ$8.50). The prime species groper is becoming increasingly scarce in the Auckland market and is a notable absentee from Table 14.14 because it was not on sale at any of the outlets visited during this survey.

Further information on price levels for New Zealand fish is shown in Table 14.15, which gives export prices at the FOB level for 1987. These prices include packaging and delivery to the departure point. The price for export quality chilled snapper shows the substantial margin over wholesale prices for the local market.

TABLE 14.15
Average export prices (FOB) for four New Zealand fish 1987. All fish whole expett groper (H & G). (NZ$/Kg)*

Species	*Chilled*	*Frozen*
Snapper	10.46	5.44
John dory	6.54	3.64
Tarakihi	5.99	3.10
Groper	6.86	3.46

*Exclusive of GST

Future price trends on the New Zealand domestic market will be influenced by export prices which in turn will be partly dependent on the exchange rate.

The supply of the prime commercial species snapper and groper to the local market are unlikely to increase in the medium term. The present TACs for these species are 25 to 50 per cent lower than catches a few years ago. If any increases in the TACs are permitted as stocks rebuild they are likely to be small and gradual. Therefore both species will continue to be in restricted supply unless the export markets collapse, which is unlikely. Supplies of other traditional species such as tarakihi, mullet and gurnard are likely to be stable.

It is possible that there may be increasing supplies of fish from the deep water fishery sold on the local market. This is likely to be accelerated if export prices weaken; it may already be occurring for orange roughy. Also, as the deep water species become better known and more accepted by the New Zealand consumer, the premium currently enjoyed by familiar coastal species may decline. This will have more effect on the fillet market than the whole fish market.

Potential export species

Pacific fishes with potential for export to the New Zealand market will be those suitable for the market niches identified above.

For the whole fish trade to the Polynesian community in the Auckland area, suitable species would meet some or all of the following criteria:

- above average price or significant price differential;
- good keeping qualities;
- available in moderate to large quantities;
- available regularly.

Suitable fishes would include snappers, emperors, groupers, breams, rabbitfish, jacks, mullet, yellowfin. If carefully handled skipjack and parrot fishes could also be exported.

For fish to be sold in processed form or marketed directly in competition with local product, suitable Pacific species would, in addition to the above criteria, need to be similar or equivalent to a New Zealand species. This will be necessary for marketing purposes because it is unlikely that any Pacific species would be available in sufficient quantities to justify promotion as a new product in its own right. A suggested list of fishes falling into this category is given in Table 14.16.

TABLE 14.16

Pacific Islands fishes and New Zealand fishes with similar characteristics for marketing purposes.

PACIFIC FISHES		*NEW ZEALAND*	
English Name	*Scientific Name*	*English Name*	*Scientific Name*
Snappers	*Lutjanidae* (many spp)	snapper	*Chrysophrys auratus*
Breams	*Sparidae* (several spp)	snapper	*Chrysophrys auratus*
Groupers	*Epinephelus* spp	groper	*Seriola lalandi*
Mullet	*Mugil* spp	mullet	*Mugil cephalus*
Dogfish	*Mustelus Squalus* spp	rig	*Mustelus anatarcticu*

Fishes which should not be exported are large groupers, trevallies and sharks because of the possibility of high mercury levels. Similarly, species in which ciguatera is known to occur should be avoided. As such species are easily identified problems should not arise.

Transport and packaging

All the FFA states mentioned in this report have at least a weekly flight to Auckland. Not all have non-stop flights but in no cases would transshipment be required. Air links between Auckland and Western Samoa, Tonga and Fiji can be considered permanent because of the volume of traffic. Direct flights to Vanuatu cannot be considered permanent as they have not always been available in the recent past. Future changes may also affect the service to Solomon Islands.

If any trade in air freighted fish is to develop it will depend on an economic commodity rate being negotiated. The published standard freights offered by airlines would make it quite uneconomic to air freight fish. Nevertheless many thousands of tonnes are so transported throughout the world each year. There is also a substantial trade in fruit and vegetables from some Pacific islands to New Zealand. Air freighted taro from Western Samoa is commonly available in Auckland and retails in the price range NZ$2.20 to $2.90/kg. The value of fish being much higher than this, it should more easily be able to support the cost of air freight.

Packaging requirements for the New Zealand market are not as demanding as for Japan where moulded polystyrene boxes are essential.

For places with non-stop flights to Auckland packing in cardboard boxes (wet lock type) with plastic liners would be adequate. Fish should be kept chilled until loading and cleared immediately on arrival to a cool store. This system is used for the carriage of chilled snapper from Fiji to Hawaii and has proved satisfactory.

If the flight involves stop-overs this sytem may not be adequate. The fish will gain heat while the aircraft is on the ground and there is always the possibility of flight delays. It would therefore seem advisable to use insulated packaging. This could be either a re-usable box or a collapsible type made up before use.

Government regulations

New Zealand Health Department regulations require the following information to be shown on the box or packaging.

(1) name and address of exporter responsible for the fish (full street address is needed, not Post Office box number);
(2) alternatively the name and address of the importer can be shown if he agrees to accept responsibility for the fish;
(3) name of the product;
(4) weight.

The Health Department has a random programme of inspection and testing of imported foodstuffs. Testing for mercury content may be required.

The permitted maximum level is 0.5ppm. This is not an average level (as in Australia) but an individual level.

The Food Regulation 1984 and its two subsequent amendments control health aspects of food in New Zealand and should be obtained if more detailed information is required. The Health Department stresses that correct labelling is very important.

There are no quarantine restrictions on the importation of fish for food. The importation of live animals is not permitted without specific approval. This could affect possible imports of live crustaceans (lobsters, crabs).

There is no customs duty on fish imports which are free from import licensing requirements. Most goods from the Pacific Islands enter New Zealand duty free under the SPARTECA agreement.

GST at the rate of 10 per cent is payable by the importer. This is levied on the C and F value plus insurance or other fees charged.

Exchange rates

A factor greatly affecting the economics of exporting to New Zealand is the exchange rate between the currencies of FFA states and the NZ dollar. Reference to the countries considered in this section over the last three years show that all of them have depreciated against the NZ dollar, which is now at recent historically high levels. Since the first quarter of 1985 the NZ dollar has appreciated by 23 per cent against the Western Samoa tala, 39 per cent against the Tonga paanga, 45 per cent against the Vanuatu vatu, 81 per cent against the Fiji dollar and 111 per cent against the Solomon Islands dollar. While the high value of the NZ dollar makes exporting there more profitable some caution would seem desirable in developing an export trade which is sensitive to exchange rate fluctuations.

Importers

Seafoods imported to New Zealand are mostly in cans or other highly processed forms. There is very little fresh or frozen product imported apart from prawns and a few other specialty lines not available from local suppliers. Many New Zealand fish traders are substantial exporters of most kinds of seafoods but have little experience of importing. Therefore to find suitable importers for Pacific fish is not as easy as in Australia, USA or Japan.

8918

Effects of Nonrandomness on Line Transect Estimates of Dolphin School Abundance

Elizabeth F. Edwards and Pierre M. Kleiber

ABSTRACT: Line transect analysis is a census method that has been used to derive estimates of dolphin school abundance from sightings data collected by observers on tuna purse seine vessels. The method is based on the assumption that movements of the sighting platform (tuna vessel) and sighted objects (dolphin schools) are random with respect to each other. In practice, neither schools nor vessels move randomly. Stratification of sightings data has been used to alleviate partially the effects of this nonrandomness, but the effectiveness of this stratification cannot be tested with data from commercial vessels because the movements of the vessels cannot be controlled.

As an alternative, we have used a relatively simple mathematical simulation model to investigate the severity of bias introduced into school abundance estimates by nonrandom movements of schools and vessels, and by the data stratification procedure. Simulations show that nonrandom movements on a scale of a few hundred miles, coupled with the data stratification procedure, can lead to overestimates of dolphin school abundance by as much as a factor of two. These results focus attention on the need to understand patterns of dolphin school distribution in smaller scales of space and time than have been studied previously, and to develop data stratification methods more robust against the effects of small-scale nonrandomness.

The National Marine Fisheries Service (NMFS) monitors mortality of dolphins involved in fishing operations by the United States purse seine fleet for yellowfin tuna, *Thunnus albacares*, in the eastern tropical Pacific Ocean (ETP), to determine whether mortality has exceeded an annual quota implemented by an act of the U.S. Congress. The quota levels depend upon whether dolphin populations are thought to be increasing or decreasing in number, relative to population levels during previous years.

The most effective method currently available for detecting trends in relative abundance is analysis of population abundance estimates collected over a period of 5–15 years. The most effective method currently available for making these abundance estimates is line transect analysis of dolphin school sightings data (Holt 1987; Buckland and Anganuzzi 1988). Two data sources are available for these line transect estimates of abundance: 1) data collected by observers during research surveys (RSOD—Research Survey Observer Data) and 2) data collected by observers during commercial fishing operations (TVOD—Tuna Vessel Observer Data). NMFS has used RSOD because research surveys can be designed specifically to satisfy the assumptions required by line transect analysis (Smith[1]). However, research surveys are very expensive and are becoming more so. This expense causes RSOD to be sparse relative to TVOD and possibly unavailable in the future.

TVOD are a potential solution to these problems, having three significant advantages over RSOD: TVOD are much more abundant, are relatively inexpensive, and are likely to continue being collected as long as fishermen set on and kill dolphins. Observer-days from tuna vessels account for roughly 95% of the annual observer effort in the ETP, while observer-days from research vessels account for only 5%. TVOD are inexpensive relative to RSOD because TVOD are collected by the observers in addition to monitoring dolphin mortality, the latter being the main reason the observer program was initiated. This monitoring program has been in operation for the past 14 years, will continue into the foreseeable future, and monitors about 30% of trips by purse seiners (both U.S. and non-U.S. vessels) each year in the ETP[2]. Ideally, TVOD could be used in place of RSOD to monitor changes in abundance of dolphins.

Elizabeth F. Edwards and **Pierre M. Kleiber**, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[1] Smith, T. D. 1975. Estimates of sizes of two populations of porpoise (*Stenella*) in the eastern tropical Pacific Ocean. Admin. Rep. No. LJ-75-67. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA.

[2] Inter-American Tropical Tuna Commission, Annual Reports 1980–1988. Scripps Institution of Oceanography, La Jolla, CA 92038.

Manuscript accepted April 1989.
Fishery Bulletin, U.S. 87: 859–876.

Reluctance to use TVOD to monitor the relative abundance of dolphins stem from concerns that TVOD 1) seriously violate some of the fundamental assumptions of line transect analysis (Polachek 1983), 2) are subject to serious but unquantified and possibly inconsistent biases, and 3) may be plagued with artifacts arising from the data collection process. Artifacts include, for example, differences between RSOD and TVOD in the sighting frequencies of various dolphin species reported by observers on research vessels compared to tuna vessels (Barlow and Holt[3]), environmental factors affecting sighting ability (e.g., sun glare, sea state, and cloud cover; Holt and Cologne 1987), and shifting areas of concentrated search effort (Buckland and Anganuzzi 1988). However, problems of this type are common to most commercial fisheries data and analyses derived from them. It is important to determine whether, despite these difficulties, useful estimates can be derived from such data sets.

Toward this end, we have developed a relatively simple model simulating the TVOD collection process. Our purpose in developing the model was twofold: 1) to test the effect of suspected biasing factors on line transect estimates of abundance and 2) to test new methods of abundance estimation prior to conducting expensive field tests. There are two unique advantages of simulation modeling in this context. First, we are simulating dolphin abundances and vessel movements within the model itself; therefore, we have available the "truth" against which to compare our model-generated estimates of abundance. Second, we have the capability of investigating effects on estimates that are due to combinations of biasing factors which may not have occurred during the years we happen to have been collecting data, but which can be expected to occur. Biasing factors include, for example, small-scale nonrandomness in school and vessel movements and spatial distributions, choice of data stratification method, changes in fishing objectives, practices, and areas of concentrated search, and changes in sighting protocol and recording procedures. We chose to focus first on the effects of nonrandomness and on the method of data stratification because recently developed methods of line transect analysis to estimate dolphin abundance from TVOD (Buckland and Anganuzzi 1988) raised serious but unanswered questions about the effects of these factors on the abundance estimates derived.

The philosophy behind building a relatively simple model was that biases shown to be troublesome and methods shown to be inadequate in a simple computer model are likely to be even more troublesome and inadequate in the real world. It is both more efficient and more economical to investigate these biases and methods first with a simple simulation model, prior to developing expensive field experiments. We have specifically applied the tenets of Occam's Razor in developing this model, making it as simple as possible while still incorporating the major processes and features contributing to the TVOD data collection process. In this study, we focused only on estimating abundance of dolphin *schools*, leaving questions about abundance of *individual* dolphins for a later day. We also assumed that data were collected without artifacts, leaving also that problem for a later set of simulations. Both of these omissions are examples of factors that probably have strong effects on analyses of TVOD, but which are at this stage unnecessary refinements to the simulation model. Such refinements could be added later if no problems were identified during simulations with the early, most simplified versions of the model.

This paper presents results of testing one hypothesis about one of the most fundamental factors suspected to affect seriously line transect estimates of dolphin abundance derived from TVOD. Specifically, we tested the effect of nonrandom clustering by dolphin schools on abundance estimates. As part of this analysis we tested also the effects of three types of data stratification prior to line transect estimation of school abundance: 1) no stratification, 2) stratification by raw encounter rate per 1° square, and 3) stratification by smoothed encounter rate per 1° square, using the smoothing and interpolation algorithm developed by the Inter-American Tropical Tuna Commission for deriving estimates of dolphin abundance from line transect analysis of TVOD (Buckland and Anganuzzi 1988). We were primarily interested in the third type of stratification, because the properties of the smoothing algorithm are poorly understood. The other two stratifications were conducted to provide a basis for comparison with the smoothing procedure.

---

[3] Barlow, J., and R. S. Holt. 1986. Geographic distributions of species proportions for dolphins in the eastern tropical Pacific. Admin. Rep. No. LJ-84-27. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA.

THE MODEL

Model Structure

This section presents a general description of model structure. A detailed technical explanation of the model can be found in Kleiber and Edwards[4]. The model (TOPS: Tuna-vessel Observer Program Simulator) simulates the movements of 75 tuna purse seiners and either 2,500 or 1,250 dolphin schools within a 1,200 × 1,200 square nautical mile area. Figure 1 provides a graphical comparison of the "study area" simulated by the model, to the entire area within which the tuna-dolphin association is exploited by the purse seine fleet. Twenty-five hundred dolphin schools is the nominal number of schools expected within a 1,200 × 1,200 nmi area of the ETP, based on Holt's (1985,[5,6] 1987) estimates of the total number of dolphins, average size of dolphin schools, and species proportions for the ETP, prorated from the entire ETP to an area 1,200 × 1,200 nmi. Simulations were also run with half this number of schools to investigate the ability of abundance estimates derived under different conditions to reflect changes in actual abundance in the model. Number of vessels is based on reported size of the ETP purse seine fleet, assuming about 50% of the fleet will be fishing a given area of this size at any one time (see IATTC Annual Reports 1983–87).

All dolphin schools are assumed to be identical (i.e., are replicates); all schools include only the

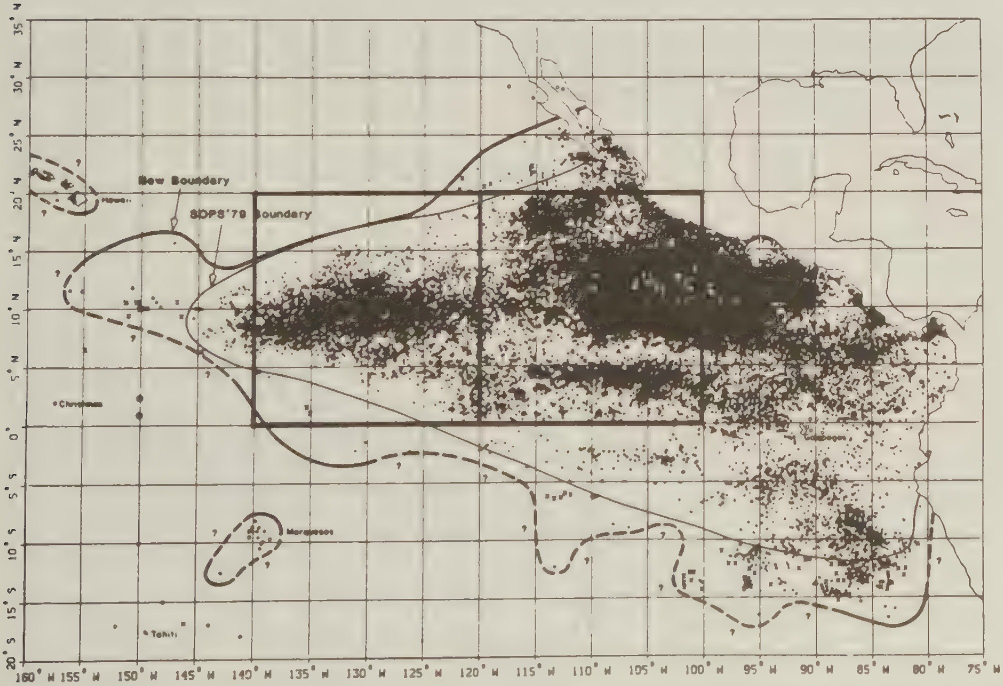


FIGURE 1.—Approximate extent of the eastern tropical Pacific Ocean (ETP) tuna purse seine fishery. Boxes enclose two areas the size of the area simulated by TOPS (1,200 × 1,200 nmi), indicating relative sizes of the entire fishery area compared to the area encompassed by the simulation.

---

[4] Kleiber, P. K., and E. F. Edwards. 1988. A model of tuna vessel and dolphin school movement in the eastern tropical Pacific Ocean: technical description of the model. Admin. Rep. No. LJ-88-28. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA.

[5] Holt, R. S. 1985. Estimates of abundance of dolphin stocks taken incidentally in the eastern tropical Pacific yellowfin fishery. Admin. Rep. No. LJ-85-16. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA.

[6] Holt, R. S. 1985. Estimates of population size of dolphins in the eastern tropical Pacific using line transect methods. Admin. Rep. No. LJ-85-20. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA.

northern offshore stock of spotted dolphins, *Stenella attenuata*, all have the same number of animals, all are equally visible, and all move independently of each other. All vessels are assumed to be identical also; they are the same size, are equally adept at sighting dolphin schools, and do not communicate with each other. Dolphin schools move at speeds varying between 0.5 and 2.4 knots, depending on conditions of the local environment (see below). All vessels move at 15 knots continuously. Speeds are based on reported averages for dolphin schools (Perrin 1979) and for vessels (vessel activity records, NMFS data bases). Vessels are assumed to chase and set upon all sighted schools. Vessels that have set on a school are "removed" from the simulation for 5 hours, simulating the average time to chase, set, collect tuna, release dolphins, and get back under way. Sighted schools are removed from the position of sighting and replaced randomly within 0 to 50 nmi of the sighting, simulating a variable "rest" period of 0 to 24 hours between one set and the next for sighted schools.

Dolphin schools move in response to the local height and gradient of an "environmental topography". The topography is a grid of equally spaced peaks of good habitat interrupted by valleys of low-quality habitat. Habitat quality varies between a value of 1 at the peaks for optimum habitats to 0 at the least favorable habitats midway between peaks. Topographies are generated as a function of sine waves in two-dimensional space and are either stationary or made to slide from right to left at 1 knot. Two combinations of peak spacing and peak shape were used for the simulations reported here: 1) a simple topography of 4 equally spaced peaks with relatively gentle slopes (Fig. 2a), and 2) a more complex topography of 16 equally spaced peaks with relatively steep slopes (Fig. 2b).

These choices for peak number generate spaces between peak tops of 300 and 600 miles. These spacings were chosen based on approximate distances between clusters of dolphin school sightings from research vessel data[7]. Peak steepness was chosen to simulate either slow spatial changes in environmental conditions (gentle slope) or rapidly changing conditions (steep slope) such as those which pertain at ocean fronts (Owen 1981).

Spacings of 600 miles between gently sloping peaks generates distances of 300 miles between maximum and minimum values of the environ-

---

[7] R. S. Holt, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. July 1987.

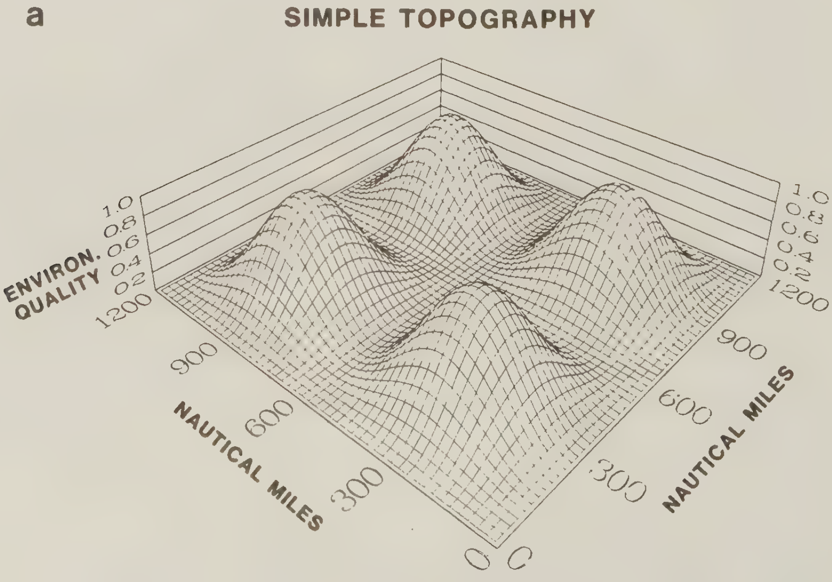


FIGURE 2.—Geometric configuration of the simple environmental

mental topography, representing a 300 mile gradual gradient from "best" to "worst" conditions (Fig. 2a). In the complex, steep environment the precipitous slopes generate a distance of only about 75 miles between maximum and minimum values for environmental quality, the slopes being separated by a "desert" of unfavorable habitat about 150 miles wide (Fig. 2b).

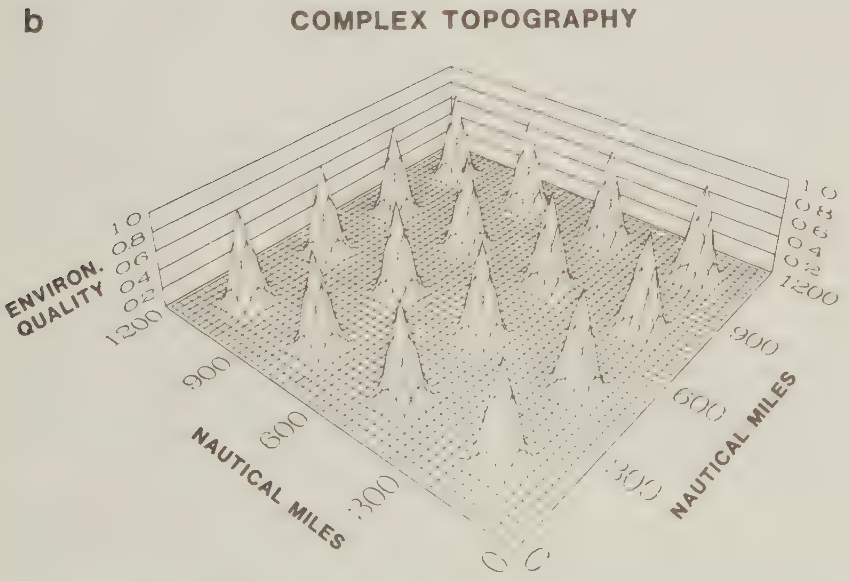
These two topographies were chosen to *bracket* a range of reasonable possibilities for patterns in environmental characteristics that may cause nonrandom clustering of dolphin schools. The factors of peak gradient and peak spacing (number of peaks) are confounded here because we tested only the two topographies, simple:gentle and complex:steep. Gentle gradients are confounded with few peaks; steep gradients are confounded with many peaks. We did not test the other two possibilities (simple:steep and complex:gentle) because these are both intermediate topographies that would have generated intermediate results. In the interest of simplicity, we restrict this simulation study to the two extreme cases.

The rate at which the topography moved (1 knot) was chosen to simulate movement of major habitat features affecting dolphin school movements. Because direct identification and measurements of such features have yet to be made, the choice of rate was based on reported speeds of major ocean currents in the eastern tropical Pacific and apparent seasonal movements of major concentrations of dolphin schools. Reported current speeds include 0.1 to 0.3 knots for the core of the Pacific North Equatorial Current bordering the fishery area on the north (Seckel 1975), 1.2 to 2.4 knots for the equatorial undercurrent underlying the fishery area (Wyrtki 1966), and 1.2 to 2.4 knots for maximum speed of the Equatorial Countercurrent surface waters encompassing a majority of the fishing area (Wyrtki 1966). School sightings data from research ships indicate that major concentrations of dolphin schools may move seasonally between distant areas at approximately 0.3 knots (200 nmi/mo)[8].

Our choice of 1 knot was based on the assumption that the mechanism(s) responsible for aggregating dolphin schools are most probably related to distributions of prey and water mass signatures indicating presence or absence of the prey. Dolphins in the ETP consume small (10–50 cm) fish and squid (Perrin et al. 1973). This mobile prey base will in turn be responding to

---

[8] S. B. Reilly, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. December 1987.



topography (a) and the complex topography (b).

movements of its own prey base of smaller animals. We reasoned that it is unlikely that this food chain is being swept along as rapidly as the maximum current speeds, but, especially on smaller scales, the distributions of prey and predator are probably moving faster than the speeds apparently characteristic of large-scale seasonal movements. We chose 1 knot as a conservative approximation. It is possible that dolphin aggregating mechanisms move, overall, more slowly than 1 knot, but probably not faster. Thus by comparing simulation results from nonmoving topographies versus topographies moving at 1 knot, we have tried to bracket the range of responses likely to occur in the real system.

In our model, dolphin schools were made to respond to these topographies by adjusting their *speed* according to the quality *level* and by adjusting their *direction* according to the gradient in quality experienced during the previous time step. The range of speeds chosen for dolphin schools (0.5 to 2.4 knots) was based on average observed cruising speeds of dolphin schools in the ETP[9]. In the model, dolphin speed is fastest at the lowest quality levels and slowest at the highest quality levels. Direction choice is stochastic with probabilities biased in the forward direction when the gradient is positive (conditions improving) and in the reverse direction when the gradient is negative (conditions deteriorating). Thus the rules for school speed and direction cause schools to circle slowly in "favorable" areas (i.e., on the peaks) and to move rapidly straight ahead in "unfavorable" areas (i.e., the valleys between peaks).

Vessel movements were controlled by each vessel's history of dolphin school sightings, through a "sightings memory" variable. The value of the variable increases by one unit each time a school is sighted and it decays constantly by a given proportion with each time step. Thus, the value of the variable will be high when a vessel is in a "good" area (i.e., has seen lots of schools) and will be low when the vessel is in a "bad" area (schools are few). Vessel direction is stochastic and affected by the value of this "sightings memory" variable. When the value is high, direction choice is biased in the reverse direction; i.e., the vessel is most likely to turn approximately 180 degrees. When the value is low, small angles are much more likely to be chosen; i.e., the vessel will tend to continue moving forward. Each vessel maintains its own sightings variable independent of the sightings variables of other vessels, so that each vessel moves independently of all other vessels.

Generation of Simulated TVOD

Each simulation began with totally random distributions of both vessels and dolphin schools. Nonrandom spatial distributions of vessels and schools then developed as a function of the environmental topography and of the movement rules for schools and vessels. Each simulation continued for 600 time steps of 1 h/step.

Estimates of school abundance were based only on TVOD collected during the last 200 steps. By this time, the model had in all cases settled into a quasi-steady state (Fig. 3). TVOD for each vessel, collected during each of these last 200 steps, included vessel number, total number of miles searched during that step, position of the vessel at the end of the step, and presence or absence of a school sighting. Only one school could be sighted per vessel per time step.

TVOD were "collected" for all dolphin schools moving within 2 nmi of any vessel. Two nautical miles is the effective strip width found commonly with line transect analyses of real TVOD.[10] All vessels were assumed to carry observers. Observers were always on duty collecting data (i.e., were never "off effort"). Vessels searched continuously (i.e., did not stop at "night").

Data Analyses

TVOD were aggregated subsequently into 1° squares prior to abundance estimation. One-degree squares are the smallest geographic subdivision that retains, with real TVOD, sufficient data for line transect analysis (Polachek 1983; Buckland and Anganuzzi 1988).

Four replicated simulations were conducted for each of eight different cases representing two

---

[9] Hedgepeth, J. 1985. Database for dolphin tagging operations in the eastern tropical Pacific, 1969–1978, with discussion of 1978 tagging results. Admin. Rep. No. LJ-85-03. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA.

[10] M. Hall, Inter-American Tropical Tuna Commission, c/o Scripps Institution of Oceanography, La Jolla, CA 92093, pers. commun.

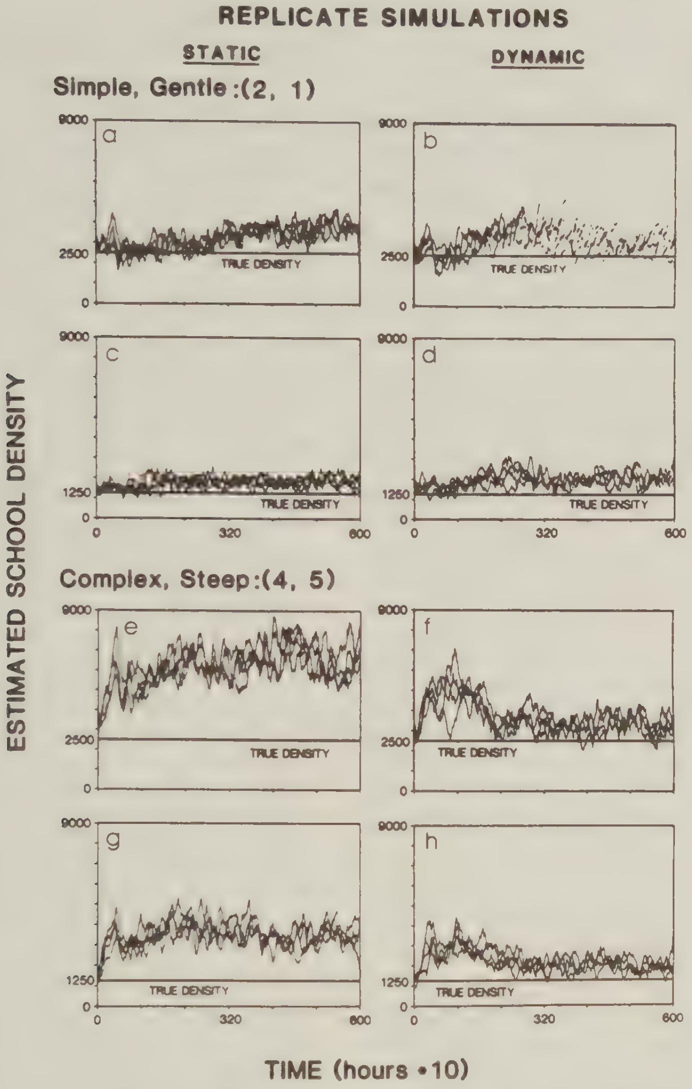


FIGURE 3.—Time course of total school abundance estimates derived from unstratified TVOD. Estimates were derived during each of 600 time steps for 4 replicated runs of 8 different starting conditions. The cases differed in environmental topography (simple, gentle vs. complex, steep), in whether the topography was static or dynamic (sliding left at 1 knot), and in underlying abundance of dolphin schools (1,250 or 2,500). Numbers in parentheses (2, 1; 4, 5) are parameters used in the equations generating the topographies.

levels for each of three factors. The factors and levels included 1) complexity of the environmental topography (simple, with 4 gently sloping peaks vs. complex, with 16 steeply sloping peaks), 2) topography dynamics (static vs. moving at 1 knot) and 3) dolphin school abundance (2,500 vs. 1,250 schools). Topography movement was implemented by causing the grid of peaks and valleys to slide uniformly sideways from "right" to "left".

Stratification Schemes

TVOD collected under each of the eight cases were subjected to three types of stratification: 1) none, 2) raw encounter rate, and 3) smoothed encounter rate.

In the case of no stratification, school abundance was estimated simply as

$$(TE/AS) * (TA) \qquad (1)$$

where TE is total number encounters by all vessels during time steps 400 to 600, AS is total area searched during that time, and TA is total area simulated (1,200 × 1,200 nmi). In this case, all 1° squares were treated as a single group or stratum.

In stratifying by raw encounter rate, encounter rates (schools encountered per nautical miles searched during the last 200 time steps) were calculated for each 1° square. The squares were subsequently ranked in ascending order of encounter rate, and grouped into (n) strata. Strata were demarcated on the basis of including at least (m) schools (encounters) per stratum. Both (n) and (m) were calculated using an algorithm developed by the Inter-American Tropical Tuna Commission for their line transect analyses of dolphin abundance in the ETP (Buckland and Anganuzzi 1988). School abundance was then estimated for each stratum separately. Total school abundance in the entire 1,200 × 1,200 nmi area was then estimated simply as the sum of these estimates per stratum.

In stratifying by smoothed encounter rate, encounter rates in each 1° square were smoothed according to the algorithms developed by Buckland and Anganuzzi (1988). Squares were then ranked and assigned to strata based on these smoothed encounter rates. This smoothing algorithm generally creates strata composed of contiguous areas of squares, arrayed in decreasing order from area of apparent high density to areas of lower density. It is not uncommon, however, for some squares in a given strata to be scattered in areas isolated from the majority for that stratum.

The smoothed encounter rates generated by the algorithm were used only during this stratification step; school abundances were estimated for each stratum using the raw (actual) encounter rate. Total abundance of dolphin schools was then estimated as the sum of the estimates for each stratum.

Estimates Derived

Two types of estimates were derived from these simulated TVOD: *total* abundance of dolphin schools in the entire simulated area, and *change* in school abundance from one sampling period to another, where this change was estimated simply as the ratio of school abundance estimates derived under two different sets of initial conditions in the model. Thus, school abundances were estimated first, and change estimates derived subsequently from these abundances. These estimates of change were calculated as a very simple analogy to a trend estimate, extending in this case over two sampling periods instead of over series of estimates. This two-sample change estimate is only a rough approximation to a trend estimate derived from a series of measurements (Gerodette 1987). However, conclusions about the effects of inconsistent biases on this *change* estimate will be valid for *trend* estimates also, except for the unlikely case in which effects of various inconsistent biases cancel each other out, so that the trend estimate reflects the actual trend, but only fortuitously.

Change estimates were derived under two conditions. Under the first condition the estimate was simply the ratio of the abundance estimate when true density was 1,250 schools (low density) to the estimate when the true density was 2,500 schools (high density). All other conditions in the model remained the same. This simulates the situation of consistent biases.

Under the second condition, the trend estimate was the ratio of one low-density estimate to one high-density estimate, but the ratio was constructed by selecting abundance estimates from cases which differed in other factors in addition to differing in dolphin abundance. This simulates the situation of biases being inconsistent from one sampling period to the next. Three ratios were selected from the many possibilities, to simulate three reasonable scenarios in the real ETP and to bracket a range from mild to severe inconsistencies.

The first of the three ratios was an estimate of abundance change in the simple environment, where in one case the environment was static during the sampling period and in the other the environment was moving at 1 knot. The second ratio was an estimate of abundance change coupled with a change in the environment from simple to complex (environments remaining static in both cases). The third ratio was an estimate of abundance change coupled with a change from a simple and static environment to a complex and moving environment. These three cases simulated ratio estimates of abundance changes from, for example, one year to the next, where conditions in the environment have also changed between years.

RESULTS

Development of Nonrandom Distributions

Relatively similar dynamics occurred within the four replicated runs of each of the eight cases (Fig. 3). In all cases, nonstratified estimates of total school abundance, calculated for each of the 600 time steps, developed progressively positive biases. Early during each simulation, estimates were relatively accurate. But as schools and vessels became progressively nonrandomly distributed (Fig. 3a–h), estimates deteriorated owing to the concentration of search effort by tuna vessels in the areas where dolphin school were prevalent and to the concomitant avoidance by vessels of areas with few schools.

Although positive bias developed in all cases, the degree and progression of bias was strongly influenced by environmental topography, both configuration and dynamics. Relatively little bias developed in cases where the topography was relatively noncomplex (Fig. 3a, c) or was moving at 1 knot (Fig. 3b, d, f, h). Very large biases developed in cases where the topography was complex and static (Fig. 3e, g).

School Abundance Estimates

Nonstratified estimates of total school abundance, calculated from TVOD collected during the last 200 time steps, show the positive bias indicated in the time courses shown in Figure 3. The degree of positive bias in unstratified estimates was not constant, but varied with model conditions (Fig. 4). Bias was least for the case of a simple, moving environment, slightly higher for the complex, moving environment, slightly higher again for the simple, static environment, and dramatically higher for the complex, static environment.

Estimates of school abundance based on stratification by raw encounter rate were in all cases relatively accurate, although estimates tended to be negatively biased for the cases of a simple environment (Fig. 4).

Estimates based on stratification by smoothed encounter rate also tended to be negatively biased for the cases of a simple environment (Fig. 4). The case of a complex, moving environment led to a slight positive bias in abundance estimates. But the complex, static environment led to pronounced overestimates of abundance that rivaled results from the unstratified analyses.

Reducing the underlying density of schools by half, from 2,500 to 1,250 schools, was mirrored by decreases of approximately one half in school abundance estimates (Fig. 4). Patterns of over- or underestimation under various model conditions remained consistent over both densitites. For example, the most severe bias occurred in both cases under conditions of a complex, static environmental topography.

Change Estimates

When change estimates were derived by comparing cases in which only the underlying density of schools was changed (i.e., when biases remained consistent between sampling periods) the estimates based on raw or smoothed encounter rate stratification were very accurate (Fig. 5). Estimates based on unstratified data were strongly biased but analyses of real TVOD are never conducted on unstratified data, so this case is useful only as an indication of improvement in estimation achieved by stratifying.

Inconsistent biases produced a dramatically different result. Even relatively small changes in underlying model conditions produced moderate to large biases in the change estimates. Also, these biases were neither consistently positive nor consistently negative, even within a single set of comparisons (Fig. 5).

DISCUSSION

School Abundance Estimates

Stratification

Overestimates were derived from nonstratified data in all cases because vessels (and therefore observers) spent more time (expended more effort) in areas where dolphin schools were abun-

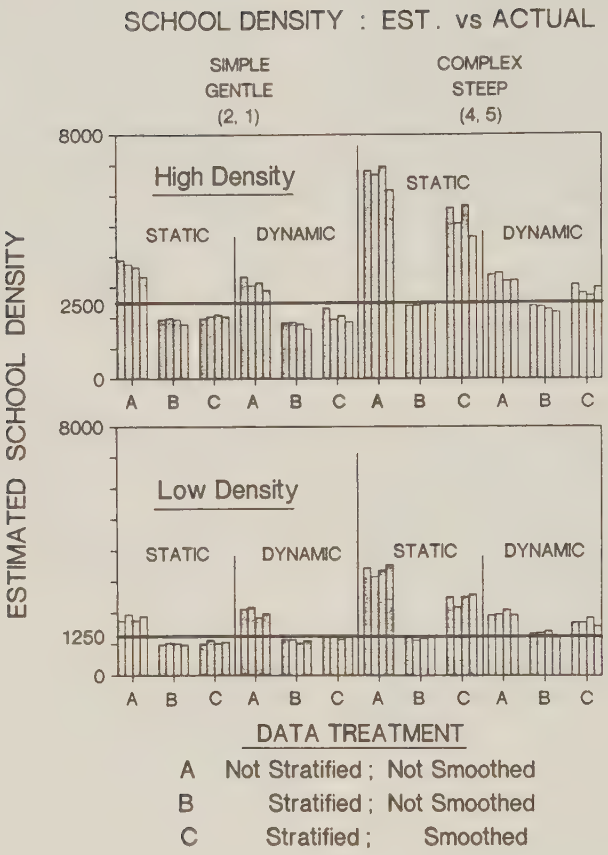


FIGURE 4.—Estimated vs. actual school density (total number of schools in simulated area) under 8 different cases for model conditions and under 3 types of data simulation for each condition. Each set of 4 columns is a set of 4 replicated runs for a given case. The cases differed in 1) environmental topography (simple, gentle vs. complex, steep), 2) whether the topography was static or dynamic (sliding left at 1 knot), and 3) actual abundance of dolphin schools (1,250 or 2,500). Numbers in parentheses (2, 1; 4, 5) are parameters used in equations generating the topographies. Two and 4 refer to the number of peaks arrayed along each axis of the spatial plane, generating a regular square grid of peaks. One and 5 are values of the parameter controlling peak slope; 1 generates a gradual slope, 5 generates a precipitous slope. Heavy lines across the figures indicate the true density (abundance) of schools in each set of simulations. Data treatments include A) no stratification before estimating school abundance, B) stratification of 1° squares based on observed (raw) encounter rates per square, and C) stratification of 1° squares based on smoothed encounter rates per square.

dant, and avoided areas where schools were few (Fig. 6). Overestimates of average school abundance per 1° square resulted from this pattern of effort because few samples from low density squares contributed to the average. Overestimates of total school abundance then followed directly by extrapolating this overestimate to the entire area.

Overestimation of school abundance was especially pronounced for the case of a complex,

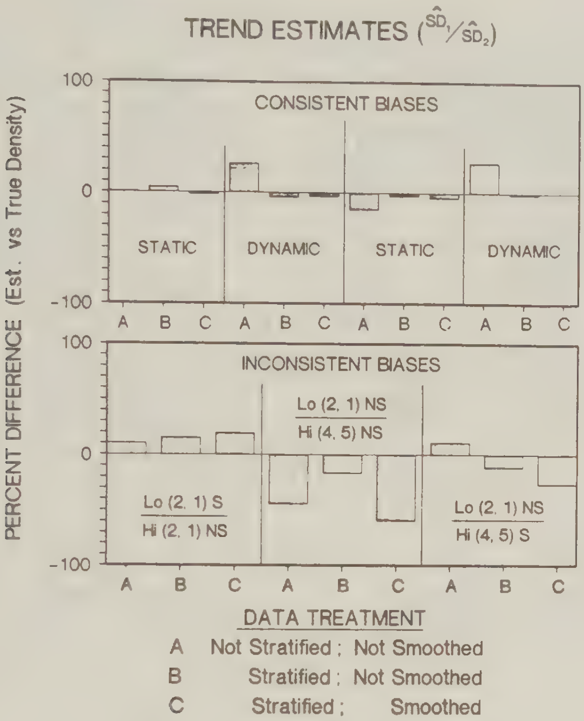


FIGURE 5.—Comparisons of estimated versus actual change ("trend") in school abundance from one sampling period to another. Changes in abundance were estimated as the ratio of school abundance (estimated or actual) under one set of model conditions (SD_1) to school abundance (estimated or actual) under some other set of conditions (SD_2). Lo and Hi refer to actual abundance of schools (Lo = 1,250 schools, Hi = 2,500 schools). S and NS refer to topography dynamics (S = topography sliding sideways at 1 knot (dynamic), NS = static topography). Number in parentheses refer to parameters generating topographies. Two and 4 refer to number of peaks along each axis. One and 5 refer to peak gradient (1 = gradual slope, 5 = precipitous slope). Three change estimates, resulting from three different types of data stratification, were generated for each comparison: A) no stratification before estimating school abundance, B) stratification of 1° squares based on observed (raw) encounter rates per square, and C) stratification of 1° squares based on smoothed encounter rates per square. Comparisons are expressed as (1 – (Estimated change/actual change))*100, so that differences appear as percentages. Differences are 0 when estimated changes equal actual changes.

static environment because this condition led to very concentrated clumping of schools within a few 1° squares. Vessels concentrated most of their effort in these few squares with very high density. Overestimates were less pronounced in the cases of a simple environment because here the areas of higher density were much more diffused and not so different from areas of low density. The gradient of increasing density toward the topographic peaks built up much more slowly, so that vessels sampled many more squares with relatively low density than had been the case for the complex, static environment. The overestimate of abundance was relatively lower for the case of the complex, dynamic environment for essentially the same reason; the

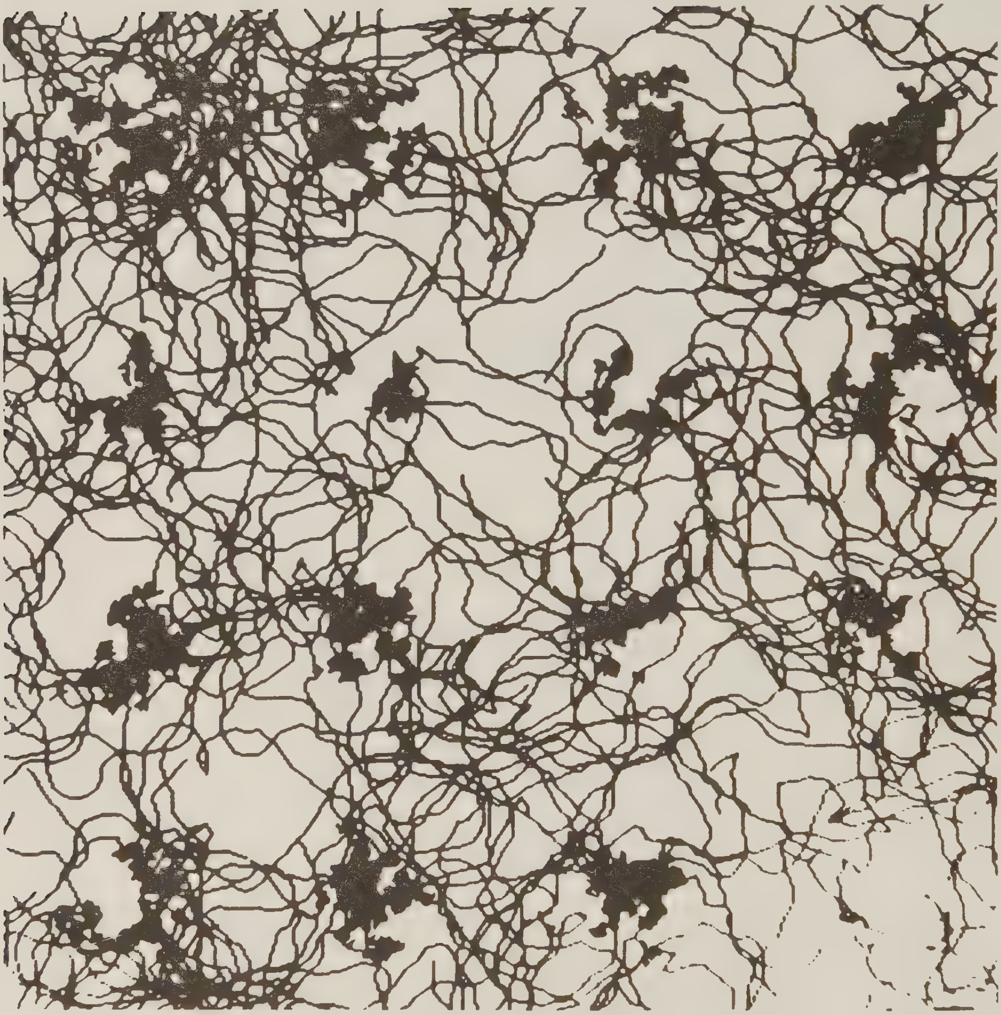


FIGURE 6.—Tracks of simulated purse seine vessels after 400 time steps during a simulation with a complex, static environmental topography. Vessel movements are concentrated near peaks in the topography, in response to the high density of dolphin schools in these areas.

characteristics of the environment produced many more squares with relatively low densitites. But here the process generating these relatively low-density squares was very different from the simple environment case. In the complex, moving environment the peaks were moving at 1 knot. Aggregating the data from the last 200 time steps generated a smeared version of the underlying 16-peak array. Integrated over the entire period of data collection, the areas of dolphin concentration appear as bands across the simulated area, rather than as individual peaks (Fig. 7). The dolphin schools spread themselves out over a larger number of squares than in the static case, producing lower estimates of average density per square.

Stratification By Raw Encounter Rate

Estimates derived from stratification by raw encounter rate were relatively unbiased in all cases because in these simulations we "collected" an unrealistically large number of TVOD with unrealistically complete coverage of the simulated area. Of the four hundred 1° squares in our 1,200 × 1,200 nmi area, no more than six went unsampled during any simulation. As a result, encounter rates in each square reflected very accurately the true school density in each square. Stratifying by these encounter rates, deriving a different estimate of average school density for each stratum, taking the weighted average of these estimates, and then extrapolating this weighted average to the entire area produced quite accurate estimates of total school abundance.

The slight negative bias in the cases of a simple environment may be due to a curious effect that was not obvious until we made a movie of vessel and school movements generated by TOPS for a simulation of the simple moving topography. It appears in this movie that vessels tend to undersample the areas of highest density in the center of the gradual peaks, because the vessels encounter enough schools along the periphery to keep them from turning into these high density, central areas. Undersampling the highest densities of course will lead to an underestimate of the average density per square and thus to an underestimate of total abundance.

This avoidance of peak centers did not occur with the complex, static environment used in our simulations, apparently because most of the peak area in this topography occurred within only a few squares (Fig. 2b). Vessel speed was apparently sufficient to carry most vessels into the highest density areas before the effects of sightings caused the vessels to slow down.

Stratification by Smoothed and Interpolated Encounter Rate

Given the apparent accuracy of estimates derived under the stratification by raw encounter rate, it would seem irrelevant to proceed to the more complicated and sometimes ineffective stratification by smoothed encounter rates. However, real world tuna vessels never sample the ETP as completely as the simulated vessels sampled the TOPS environments. In most years, fewer than half the vessels carry observers, the fleet as a whole samples less than half the entire ETP, and the sampling that is done tends to be concentrated seasonally in variable geographic areas (Buckland and Anganuzzi 1988). This leaves many 1° squares unsampled.

For management purposes, we cannot assume that squares with no effort contained no dolphins; therefore, we are left with the necessity of estimating densities in those unsampled areas. We have to fill in the holes somehow, so an interpolation method, either a more robust method than used to date, or some new method, is required.

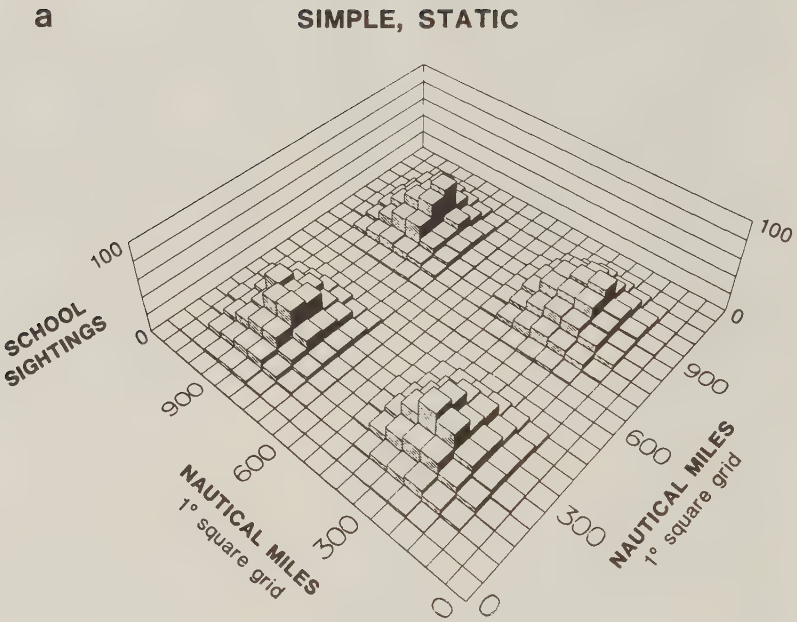
In most of the TOPS simulations, Buckland and Anganuzzi's (1988) smoothing and interpolation routines worked quite well, with accuracy rivaling that of the raw encounter rate stratification. The very poor performance of the smoothing algorithm in the case of a complex, static environment, however, is troubling because we have no data from the field to determine whether or not such topographies exist in the ETP. We suspect that such topographies do exist because the parameters used in the TOPS model were chosen specifically to be reasonable. In particular, the distances between peaks were chosen to bracket the apparent distances between clusters of dolphin schools as indicated by sightings from research vessels.[11] Also, the movement rates by vessels, schools, and topography were specifically selected to approximate observed rates.

The severe bias in the complex static case arises owing to an interaction between the effective sampling frequency (in this case, 1° squares), the peak topography, and the mechanics of the smoothing algorithm. The algorithm works by calculating, for each square, a smoothed encounter rate that is a weighted average of encounter rates for all squares within a radius of at least four squares. Thus the smoothed rate in each square is affected by rates across a diameter of at least eight 1° squares, or a distance of at least 480 nmi (8 × 60 nmi). In the case of the complex, static topography, this minimum distance is greater than the distance between peaks (300 nmi). Also, the relatively precipitous peaks encompass only 3 or 4 squares and are separated by low-density areas several squares across. The smoothing algorithm tends to "fill in" these low-density areas, elevating apparent encounter rates in the intervening squares and causing squares to be assigned to strata out of proportion to the true densities of dolphin schools in the squares.

It is possible that the relatively precipitous slopes of the peaks in the complex environment

---

[11] R. S. Holt, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. December 1987.



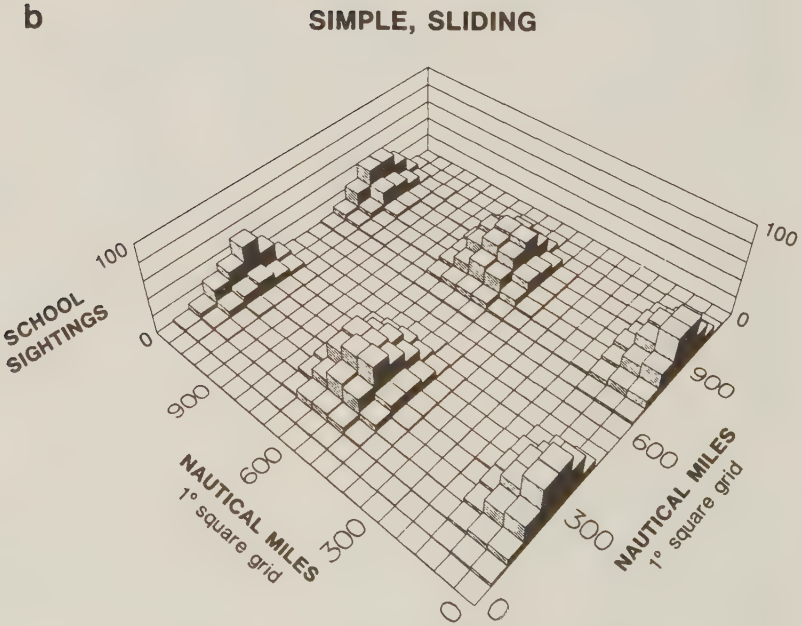
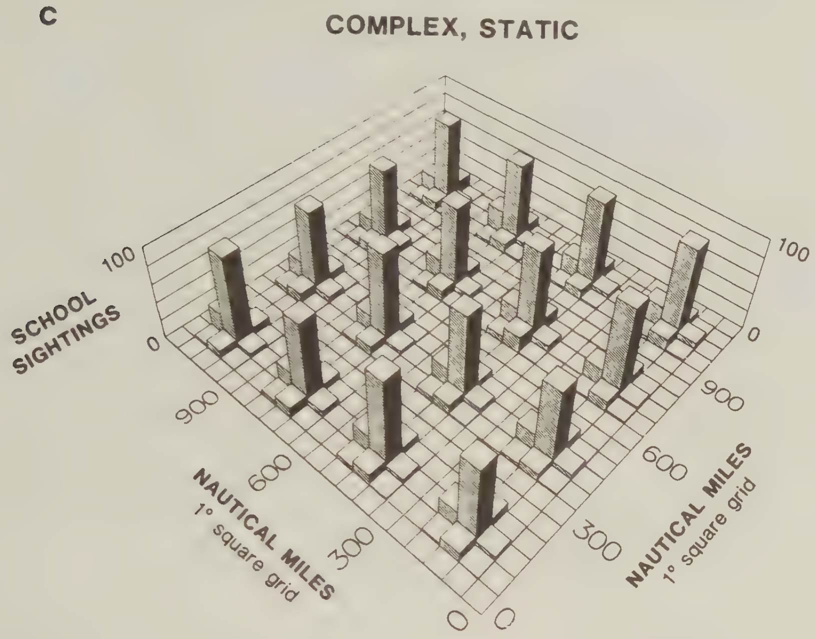
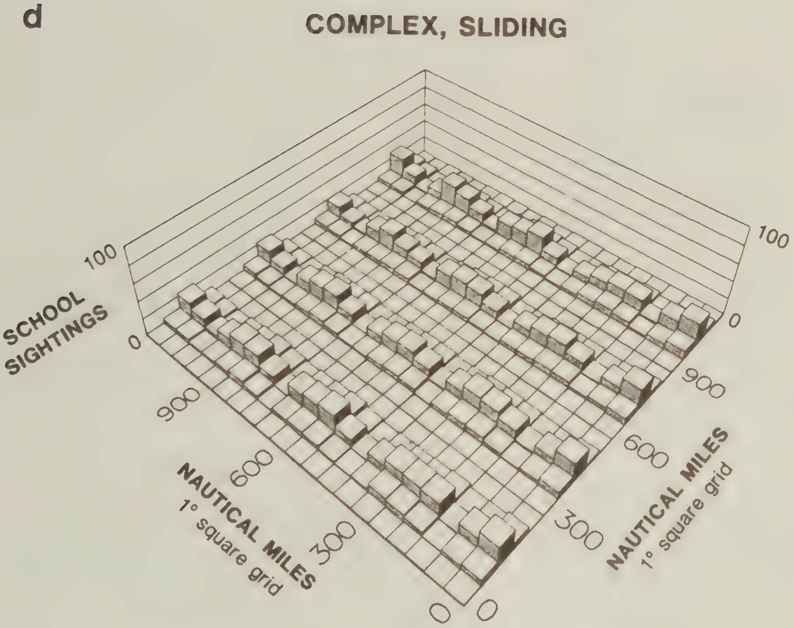


FIGURE 7.—Average number of sightings of dolphin schools per 1° square during the last 200 a) simple, static, b) simple, sliding,





time steps of one simulation for each of the four types of environmental topography
c) complex, static, and d) complex, sliding.

are unrealistic, but in fact these slopes extend over at least two 1° squares (Fig. 2b). This is a distance of at least 120 nmi. Conditions change across ocean fronts in distances much shorter than this, and ocean fronts are aggregating mechanisms for many marine biota (Owen 1981). Of course, such fronts are never static and the smoothing algorithm worked quite well in the complex, dynamic environment, apparently owing to the smearing effect discussed previously. However, as in the previous case, we have as yet insufficient data to identify the conditions actually pertaining in the real ETP.

The major point is that the simulations have shown that clustering characteristics on relatively small scales (10s to 100s of miles) can seriously bias estimates of abundance derived via the smoothing algorithm, which is a problem because as yet we know almost nothing about clustering on this scale in the real ETP. The model results indicate strongly that future research should be focused either on resolving this lack of information or on developing alternative analyses that are not as sensitive as this smoothing algorithm to these small-scale spatial effects.

Change Estimates

These demonstrated problems with estimating school abundance are serious but in real-world analyses could perhaps be ignored; the next set of dolphin quotas will be determined not on the basis of estimated absolute abundance at some point in time but rather on the basis of *estimated changes* in abundance (Holt et al. 1987). This is an advantage in the estimation process because as long as nothing other than dolphin abundance changes from one sampling period to the next (i.e., as long as biases remain consistent), then accurate estimates of those changes in abundance can be derived from TVOD.

However, we know almost as little about whether biases truly remain constant (consistent) in the ETP, as we know about small-scale spatial distributions of dolphin schools. It is obvious from Figure 5 that even relatively small changes in bias can lead to considerably inaccurate estimates of change and, by implication, estimates of trend. A change as simple as moving from a static to a slowly moving environment produced an overestimate in the ratio estimate of almost 20% (Fig. 5, Lo(2, 1)S/Hi(2, 1)NS). Not even the direction of bias remained consistent, changing from positive in some cases to negative in others.

The ratio estimate based on a simple static environment during one sampling and a complex static environment during the other period (Fig. 5) is of particular interest, because an effect of this type may be the basis for the anomalous and biologically unlikely dip in Buckland and Anganuzzi's (1988) estimates of abundance for northern offshore spotted dolphin, *Stenella attenuata* during 1983 (Fig. 8), the year of an exceptionally strong El Niño. Our simulation results in this case lead to a potentially testable hypothesis about a factor that may have significantly affected analyses of real TVOD. Preliminary analyses of apparent differences in distributions of dolphins during El Niño versus non-El Niño years support the hypothesis that changes in spatial distributions led to inconsistent biases and thus to inaccurate trend estimates during these years.[12]

SUMMARY

The results from these simulations are useful in a general sense; they show that significant biases can develop within the simple model structure used here. The quantitative results are specific to the parameter values and movement rules chosen for these particular simulations and are neither intended nor assumed to mirror specific distributions of either vessels or dolphin schools in the real environment of the ETP. Although parameter values controlling rates and abundances are "correct" to the best of our knowledge, choosing different parameters for the functions controlling dolphin responses to the environment, or vessel responses to dolphins, would probably change both the rates and spatial characteristics of pattern development and thus estimates of abundance derived.

Other clustering patterns could have been used, and other results generated. However, our purpose at this stage was not to generate a catalogue of patterns and responses. Our purpose was to test the effects of varying a simple but reasonably realistic (in terms of rates and spacings) aggregating pattern for dolphin schools, using the results to determine whether any insight could be gained into the problem of estimating abundance of dolphin schools in the real world, using real TVOD.

Indeed, we found that our simplified simula-

---

[12] S. B. Reilly, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun.

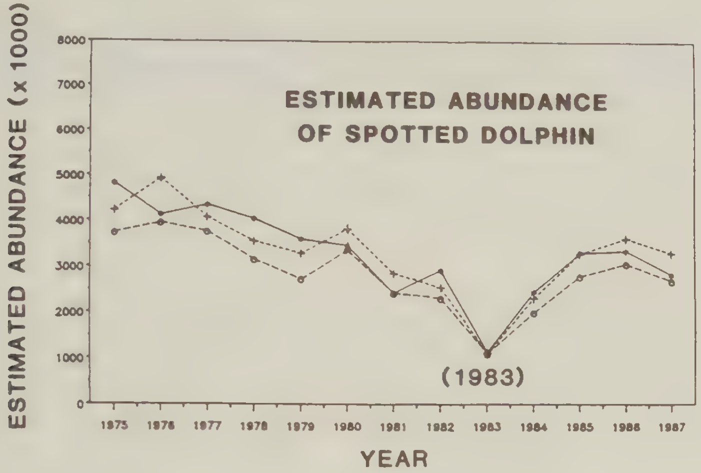


FIGURE 8.—Estimated abundance of northern offshore spotted dolphin, *Stenella attenuata*, showing biologically unlikely recovery in 1984 following apparent decrease in abundance during 1983 (from Buckland and Anganuzzi 1988).

tion approach identified two critical problems that must be addressed if TVOD are to an effective source for estimates of dolphin abundance or changes in abundance in the eastern tropical Pacific Ocean. These critical problems are 1) the effect of small-scale nonrandomness of dolphin schools, and 2) the interactions between these small-scale patterns (sampling frequency and smoothing algorithms) on estimates of school abundance or change in abundance derived from line transect analysis of sightings data. Research effort should now be directed toward identifying and characterizing school distributions within these smaller spatial (and temporal) scales, and toward improving the efficacy of existing methods or developing new methods for analyzing TVOD.

ACKNOWLEDGMENTS

Development of the model and preparation of this paper have been aided significantly by the sage advice and helpful criticisms of Steve Reilly and Doug DeMaster.

LITERATURE CITED

Buckland, S. T., and A. A. Anganuzzi.
1988. Trends in abundance of dolphins associated with tuna in the eastern tropical Pacific. Rep. Int. Whaling. Comm. 38:411–438.

Gerodette, T.
1987. A power analysis for detecting trends. Ecology 68:1364–1372.

Holt, R. S.
1987. Estimating density of dolphin schools in the eastern tropical Pacific Ocean by line transect methods. Fish. Bull., U.S. 85:419–434.

Holt, R. S., and J. Cologne.
1987. Factors affecting line transect estimates of dolphin school density. J. Wildl. Manage. 51:836–843.

Holt, R. S., T. Gerrodette, and J. Cologne.
1987. Research vessel survey design for monitoring dolphin abundance in the eastern tropical Pacific. Fish. Bull., U.S. 85:435–446.

Owen, R. W.
1981. Fronts and eddies in the sea: mechanisms, interactions, and biological effects. *In* A. R. Longhurst (editor), Analysis of marine ecosystems, p. 197–233. Acad. Press, Lond.

Perrin, W. F., R. W. Warner, C. L. Fiscus, and D. B. Holts.
1973. Stomach contents of porpoise, *Stenella* spp. and yellowfin tuna, *Thunnus albacares* in mixed-species aggregations. Fish. Bull., U.S. 71:1077–1092.

Perrin, W. F.
1979. Movements of pelagic dolphins (*Stenella* spp.) in the eastern tropical Pacific as indicated by results of tagging, with summary of tagging operations, 1969–76. U.S. Dep. Commer., NOAA Tech. Rep. NMFS, SSRF-737, 14 p.

Polachek, T.
1983. The relative abundance of dolphins in the eastern tropical Pacific based on encounter rates with tuna purse seiners. Ph.D. Thesis, Univ. Oregon, Eugene,

or, 440 p.

Seckel, G.

1975. Seasonal variability and parameterization of the Pacific north equatorial current. Deep Sea Res. 22:379–401.

Wyrtki, K.

1966. Oceanography of the eastern equatorial Pacific Ocean. Oceanogr. Mar. Biol. Annu. Rev. 4:33–68.

8919

Maturation and Reproduction in Two Hawaiian Eteline Snappers, Uku, *Aprion virescens*, and Onaga, *Etelis coruscans*

Alan R. Everson, Happy A. Williams, and Bernard M. Ito

ABSTRACT: Size at sexual maturity, spawning season, and pattern of egg release were determined for two of Hawaii's commercially important snapper species: uku, *Aprion virescens*, and onaga, *Etelis coruscans*. Sexual maturity of females was assessed by macroscopic and microscopic (oocyte measurement and histology) techniques and gonosomatic indexes. Interspecific differences were noted in many aspects of the reproductive biology. Both species had protracted spawning seasons: uku spawned in May-October while onaga spawned in June–November. Female size at sexual maturity was 425–475 mm fork length (FL) for uku and 675–725 mm FL for onaga. Both species were determined to be multiple spawners, although the number of batches spawned per season could not be established.

Uku, *Aprion virescens*, and onaga, *Etelis coruscans* (Lutjanidae), are species of considerable importance in terms of total landings and value to bottom fish fisheries in southern Japan (Masuda et al. 1975), Guam, the Northern Marianas (Amesbury and Myers 1982), Vanuatu (Brouard and Grandperrin 1985), American Samoa (Western Pacific Regional Fishery Management Council (Council) 1986), and Hawaii (Ralston and Kawamoto[1]). In addition, many other Pacific island nations have subsistence and commercial fisheries for these species. In Hawaii, uku and onaga ranked second and third, after *Pristipomoides filamentosus*, in total catch and value among bottom fish species in 1984 (Pooley 1987).

Both species are widely distributed throughout the tropical Indo-Pacific. Uku range from East Africa to Hawaii and from southern Japan to Australia (Allen 1985), and onaga extend to the Atlantic coasts of South America and Africa (Druzhinin 1970). Uku are caught at the surface by trolling gear and at ≤ 300 m depths by deep-sea handline gear (Druzhinin 1970), whereas onaga are restricted to deeper waters between 220 and 320 m. In Hawaii, the greatest portion of the uku and onaga catches comes from the Penguin Bank region, which is southwest of Molokai in the main Hawaiian Islands (Ralston[2]).

Relatively few reproductive studies have been completed for the commercially important bottom fishes of the western Pacific, even though such information represents a critical component of the biological basis of management for the bottom fish and seamount groundfish fisheries in this region (Council 1986). Some information is available on Hawaiian stocks of *P. filamentosus* (Ralston 1981; Kikkawa 1984), *Etelis carbunculus* (Everson 1984), and *Seriola dumerili* (Kikkawa and Everson 1984), but none is available for uku and onaga. Thus, a study was undertaken to determine the size at sexual maturity, spawning season, and pattern of egg release of uku and onaga. Size at sexual maturity is a particularly important parameter used to assess and evaluate the impact of fishing mortality on spawning stock biomass and to determine levels of optimum fishery yield (Polovina 1987). During this study, we also attempted, within the constraints imposed by our sampling program, to develop an efficient method for determining gonad maturity. A third goal was to discern interspecific differences between the reproductive biology of the two species and to interpret those differences.

---

[1] Ralston, S., and K. E. Kawamoto. 1987. An assessment and description of the status of bottom fish stocks in Hawaii. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396. Southwest Fish. Cent. Admin. Rep. H-87-7, 55 p.

[2] Ralston, S. 1979. A description of the bottomfish fisheries of Hawaii, American Samoa, Guam, and the Northern Marianas. A report submitted to the Western Pacific Regional Fishery Management Council, Honolulu, 102 p. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu HI 96822–2396.

Alan R. Everson, Happy A. Williams, and **Bernard M. Ito,** Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396.

Manuscript accepted May 1989.
Fishery Bulletin, U.S. 87: 877–888.

MATERIALS AND METHODS

Uku and onaga caught in 1984–86 and 1985–87, respectively, by commercial fishermen using deep-sea hook-and-line gear were weighed and measured for fork length (FL), and their capture locations were noted. Most were caught in the main Hawaiian Islands and were sold through the Honolulu wholesale fish auction. Following sale of the fish, viscera were extracted by the purchasing agent and refrigerated with an identifying tag. Gonad samples were collected later and preserved at the laboratory either in modified Gilson's fluid (Bagenal and Braum 1968) or Bouin's fluid.

Sexual maturity of females was evaluated by several methods. First, ovaries were staged macroscopically and given a preliminary maturity stage designation (Hilge 1977) (Table 1). To refine and confirm these macroscopic designations, at least one of the following three additional microscopic techniques was used: volumetric or cork borer subsampling, which is based upon the size and appearance of individual oocytes, or standard histological examination. Hilge's (1977) table was also used to assign a final stage designation to these ovaries. To avoid confusion, prespawning adults prior to vitellogenesis were classified as stage I immature, and prereproductive individuals as stage I juvenile.

To determine oocyte size-frequency distributions by volumetric subsampling, uku ovaries preserved in modified Gilson's fluid were examined. After adequate time for dissolution, connective tissues were removed, and the remaining "free" ova were placed in a flask, which was then filled with 200 mL of water. A homogeneous distribution of ova was obtained by using a magnetic stirrer (Van Dalsen 1977). A 3 mL sample was then pipetted onto a gridded petri dish and examined under a binocular dissecting scope at 50×. With an ocular micrometer, 100–200 oocytes were measured along their longest dimension. This method precluded the need to measure oocytes from various sites within the ovary to determine spatial homogeneity of development. Maturity stages were assigned based upon the largest oocyte mode and the degree of oocyte transparency (Table 1).

Subsamples of ovaries of both species preserved in Bouin's fluid were taken from the anterior portion with a cork borer and examined under a binocular dissecting microscope at 50×. The average diameter of the largest oocyte mode was determined, and the percentage of each maturity stage present was noted. Oocyte diameter frequency plots were constructed for uku ovaries in various stages of development and compared with similar plots constructed by using oocyte diameter data obtained by the volumetric method.

For histological examination, some ovaries of both species representing various visually identifiable maturity stages were transferred from Bouin's fluid to 70% ethanol. Portions of ovaries from 28 uku and 22 onaga caught at various times of the year were embedded in paraffin, sectioned at 5 μm, stained with hematoxylin, and counterstained with eosin. Each was as-

TABLE 1.—Ovary developmental stage designations used for study of the reproductive cycle of uku and onaga. Designations are adapted from Hilge (1977).

Class	Stage	Oocyte developmental status	Gonad external appearance	Stage classification criterion
I	Immature	Oogenesis from oogonium to primary oocyte with cytoplasmic vacuoles beginning to appear	Genit ridge to definite gonad; individual eggs not discernible	Oogonia transparent; primary ooctes translucent
II	Developing	Vitellogenesis	Elongation of the ovary	Opaque yolked oocytes
III	Ripe	Hydration	Swollen; ovary wall thin	Transparent, ripe ova
IV	Spent	Atresia, general cell breakdown	Slack; shrinking ovary; ovary wall thick	Residual ova

signed a maturity stage based on the criteria in Table 1. Oocytes were histologically identified using information provided in Crossland (1977). Sectioned ovaries also were examined for the presence of postovulatory follicles and oocyte atresia, features used to establish criteria for the estimation of spawning frequency and to separate juveniles from prespawning adults for determination of size at sexual maturity (Hunter and Macewicz 1985).

The results of these four visual methods were compared with gonosomatic index (GSI) values [(gonad weight/body weight) × 100]. Gonosomatic indexes were calculated for both species to provide a rapid but preliminary indication of developmental stage, although an insufficient number of uku testes were obtained. Excluded from this analysis were individuals that had not yet reached size at sexual maturity. Spearman's coefficient of rank correlation (Snedecor and Cochran 1978) was used to ascertain whether a positive relationship existed between GSI and maturity stage during the spawning periods for females of each species.

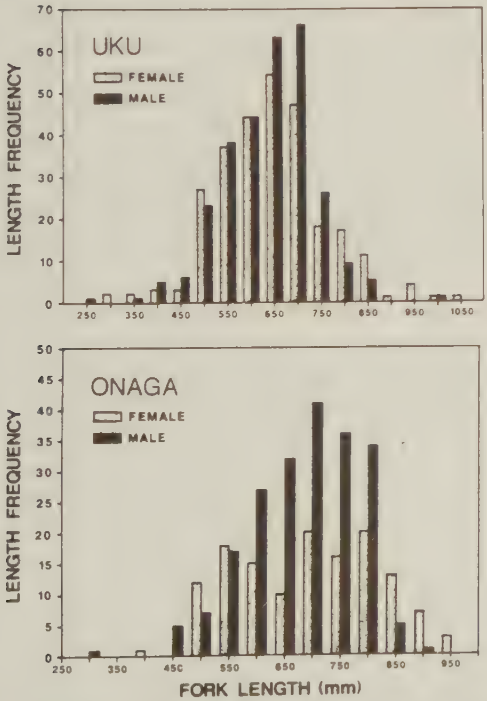


FIGURE 1.—Length-frequency distribution of male and female uku and onaga.

Size at sexual maturity (L_{50}) was defined as the smallest length category in which at least 50% of the individuals were mature (i.e., stage II or beyond, GSI > 1.5) during the spawning season. The logistic equation was fitted to the percentage of mature individuals in each size class (P_x) and FL (Gunderson et al. 1980; Ni and Sandeman 1984); that is

$$P_x = \frac{100}{1 + \exp(a\mathrm{FL} + b)},$$

where a and b are fitted parameters and $L_{50} = -b/a$. We also calculated the percentage of maximum length (MAXLEN) at which sexual maturity occurred. This ratio has been used to compare proportionate size at maturity for species by habitat type, zoographic province, or depth range (Grimes 1987).

Sex ratios were compiled and examined for significant deviation from unity and to determine whether sex ratio and size (in 50 mm FL intervals) were independent using chi-square statistics. Two-way contingency table analysis was performed to determine whether the sex ratio differed during the year when pooled into bimonthly periods.

RESULTS

Spawning Season

Spawning season was determined from a wide size range of uku and onaga (Fig. 1). The Spearman rank correlation coefficients (r_s) calculated by comparing GSI with stages I–III were $r_s = 0.6205$ for uku ($P < 0.0001$), and $r_s = 0.8685$ for onaga ($P < 0.0001$), indicating a positive relationship between GSI and stage of development for both species, although the correlation was considerably lower for uku. In addition, the range in GSI values representing stages II and III ovaries was greater for uku than for onaga (Fig. 2). Thus, rather than using GSI as the single method for estimating spawning seasonality by month or fish length, visual staging methods also were used.

Both species reached maturity in the spring and summer and spawned continuously until fall or early winter. Neither species reached stage II of development (vitellogenesis) at any other time of the year. Uku spawning began in May and peaked 1 month later in June, as evidenced by the sharp rise in GSI values and the presence of mature and ripe fish during this time (Figs. 3, 4).

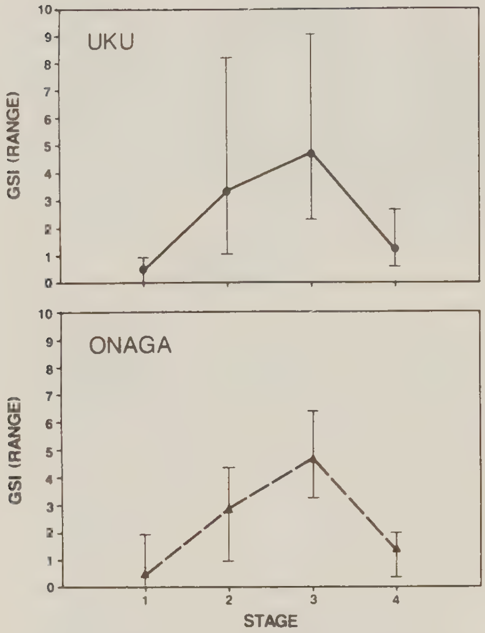


FIGURE 2.—Range in (A) uku and (B) onaga gonosomatic index (GSI) for each developmental stage designation in Table 1.

From July to October, the mean GSI values gradually decreased as spawning activity tapered off. By November, all fish examined were either partially or completely spawned (stage IV). Stage IV fish were not found during the spawning season.

In contrast, female onaga began maturing in June. Fully ripe onaga were not found until July, and spawning activity did not peak until October (Figs. 3, 4). The GSI values dropped sharply in November as the incidence of completely spawned and partially spawned individuals abruptly increased. As with uku, completely spawned individuals were not found until the close of the spawning season. Mean monthly GSI values for male onaga reflected a similar pattern.

Size at Sexual Maturity

Uku matured at a substantially smaller size than onaga. Fifty percent of the female uku attained sexual maturity at 425–475 mm FL, as evidenced by elevated GSI's (Fig. 5) and by the percentage of fish judged mature by visual staging (Table 2). By the time the fish reached the

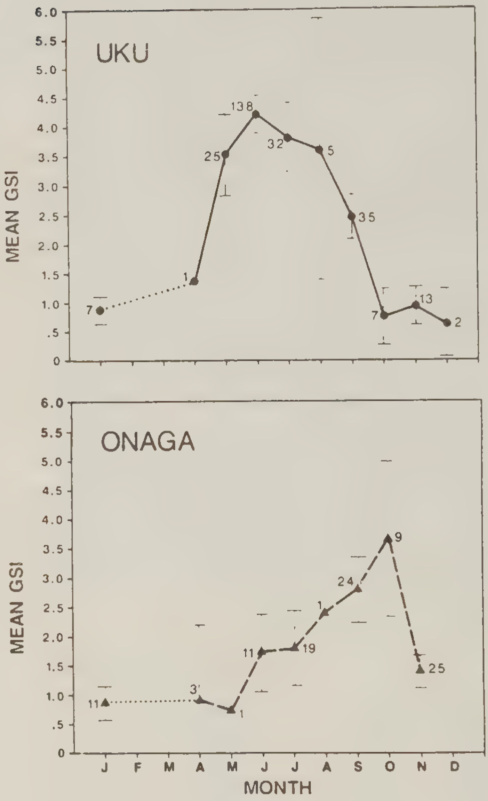


FIGURE 3.—Monthly mean gonosomatic index (GSI) for female uku and onaga. Bars indicate 95% confidence limits. Juvenile (<500 mm FL) uku and juvenile (<600 mm FL) onaga were excluded from analysis. Sample size is indicated next to each data point.

TABLE 2.—Stage of maturity, compared by 50 mm fork length (FL) size classes, for uku and onaga sampled during their respective spawning seasons.

Uku			Onaga		
FL (mm)	*N*	Percentage mature	FL (mm)	*N*	Percentage mature
275–324	2	0	475–524	11	9
325–374	1	0	525–574	15	7
375–424	2	0	575–624	12	33
425–474	3	66	625–674	4	25
475–524	12	100	675–724	13	77
525–574	21	100	725–774	13	92
575–624	18	95	775–824	16	100
625–674	20	95	825–874	6	100
675–724	15	94	875–925	5	100
725–774	4	100			
775–824	5	100			

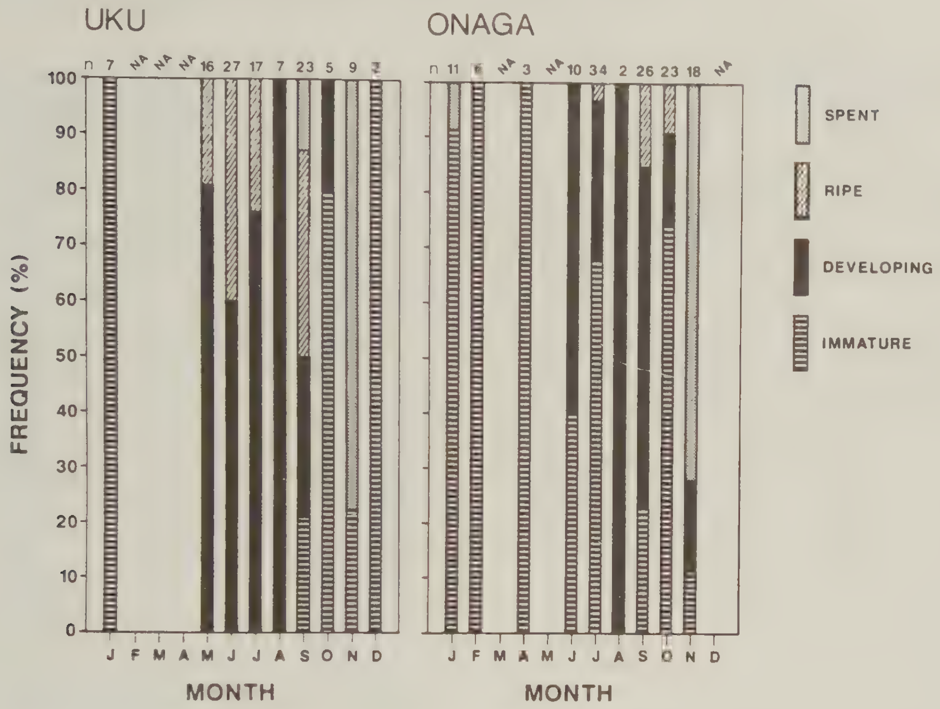


FIGURE 4.—Monthly percentages of uku and onaga ovaries at various stages of development determined by visual staging methods. N = number of samples per month.

500 mm size class, 100% were mature. The smallest uku with vitellogenic (stage II) ovaries during the spawning season was 429 mm FL (1.27 kg), which is 41.7% of the maximum length (MAXLEN) recorded for the study animals. The smallest individual with ripe (stage III) ovaries was 477 mm FL (1.82 kg) or 46.4% of the MAXLEN. The predicted value of L_{50} obtained from the logistic fit of percentage mature on FL (Fig. 6) was 449 mm FL ($a = -0.3444$, $b =$

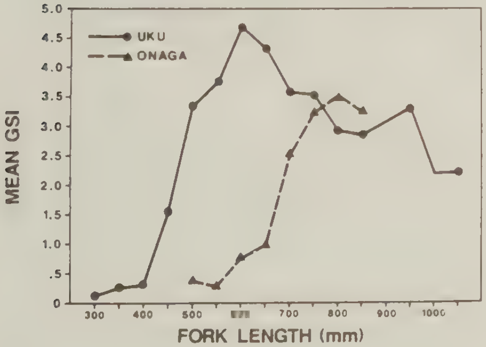


FIGURE 5.—Mean gonosomatic index (GSI) plotted by 50 mm FL intervals for female uku and onaga sampled during their respective spawning seasons.

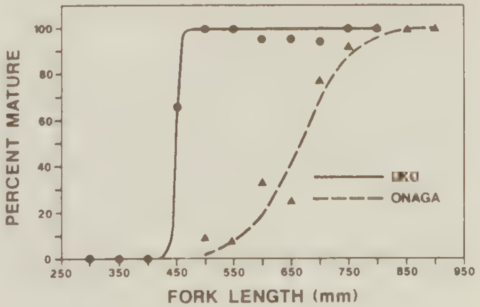


FIGURE 6.—Proportion of sexually mature female uku and onaga within each size class, plotted with the predicted proportion of mature females.

154.31). Interesting to note was the propensity for decreasing mean GSI's in uku larger than 600 mm FL (Fig. 5).

In contrast, the smallest mature onaga was 522 mm FL (2.22 kg) or 53.9% MAXLEN, and ripe individuals were not encountered until 605 mm FL (3.22 kg) or 62.4% MAXLEN. The predicted value of L_{50} obtained from the logistic fit of percentage mature on FL was 663 mm FL ($a = -0.0233$, $b = 15.462$; Fig. 6), and 77% of the onaga in the 675–725 mm FL class were found to be at stage II of development or beyond (Table 2). Onaga spawned over a narrower size range (600–900 mm FL; Fig. 5) compared with uku (450–1,050 mm FL; Fig. 5).

Histological examination of ovaries indicated that both species follow a similar pattern of development (Fig. 7). The progression from oogonia to hydration is typical of snappers and has been covered in detail by Crossland (1977) and Wallace and Selman (1981). Postovulatory follicles were not identifiable in tissue sections from ripe (stage III) ovaries of either species. None of the immature (stage I) ovaries examined histologically showed signs of atresia, indicating that these fish had not previously spawned. Identifiably atretic individuals in later stages of development were not observed until the end of the spawning season.

Spawning Frequency and Pattern of Egg Release

The size-frequency distributions of oocyte diameter were constructed for ovaries of uku caught during the spawning season, using the volumetric method, and were found to be polymodal, suggesting that uku may release multiple egg batches (Fig. 8a). All ovaries possessed a

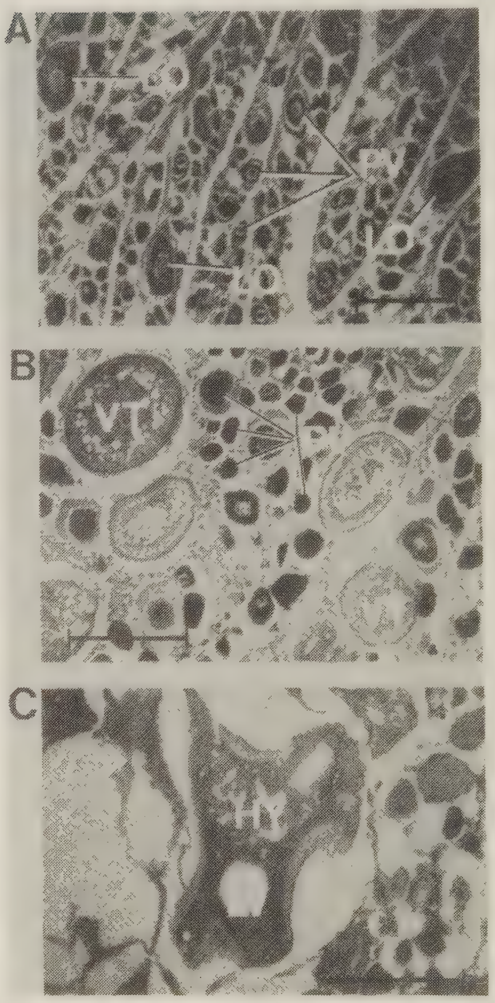
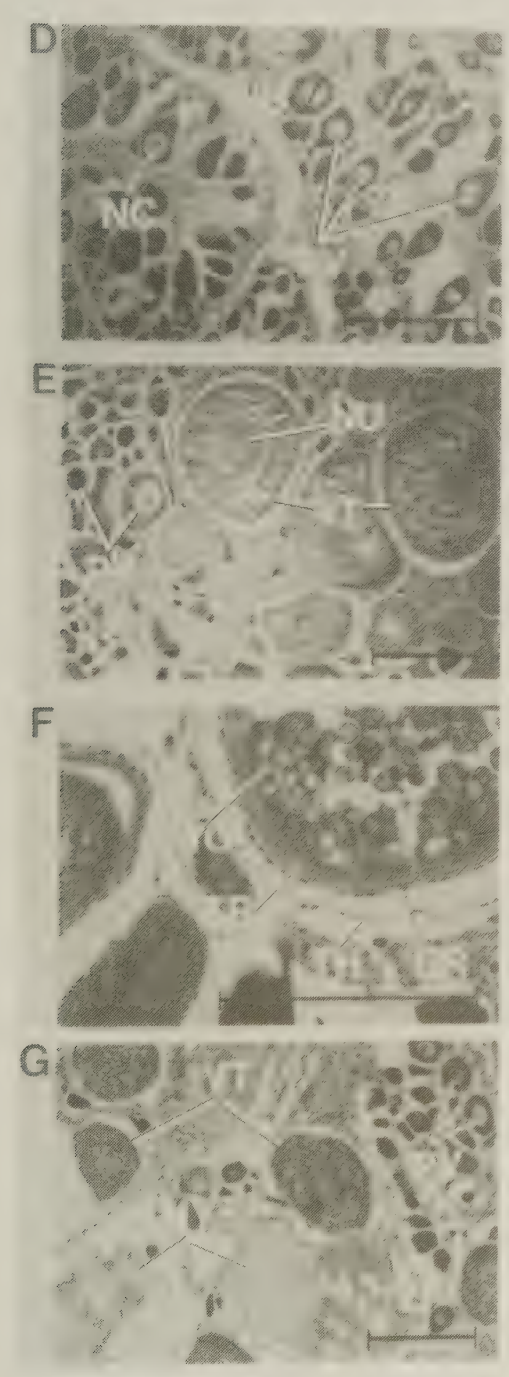


FIGURE 7.—Photomicrographs showing transverse histological sections of uku and onaga ovaries in various stages of development. Scale bars represent 0.10 mm. A. Early developing uku (386 mm FL) ovary classified as juvenile (stage I) containing numerous previtellogenic (PV) oocytes. Larger oocytes (LO) have reached the lipoid or yolk vesicle stage, just prior to vitellogenesis. B. Developing (stage II) uku (525 mm FL) ovary. Shown are previtellogenic (PV) and vitellogenic (VT) oocytes. C. Ripe (stage III) uku (541 mm FL) ovary with hydrated (HY) oocytes. Lipoid vesicles have fused to form a single mass (LV). D. Juvenile (stage I) onaga (506 mm FL) ovary consisting of previtellogenic (PV) oocytes with large central nucleus (NU) containing numerous nucleoli (NC). E. Developing (stage II) onaga (753 mm FL) ovary showing numerous mature oocytes in different stages of vitellogenesis (VT). F. Enlargement of a developing onaga ovary. Shown are granulosa (GR) and thecal (TH) cell layers, zona radiata (ZR), and yolk granules (YG). G. Ripe (stage III) onaga (605 mm FL) ovary showing hydrated (HY), vitellogenic (VT) and previtellogenic (PV) oocytes.



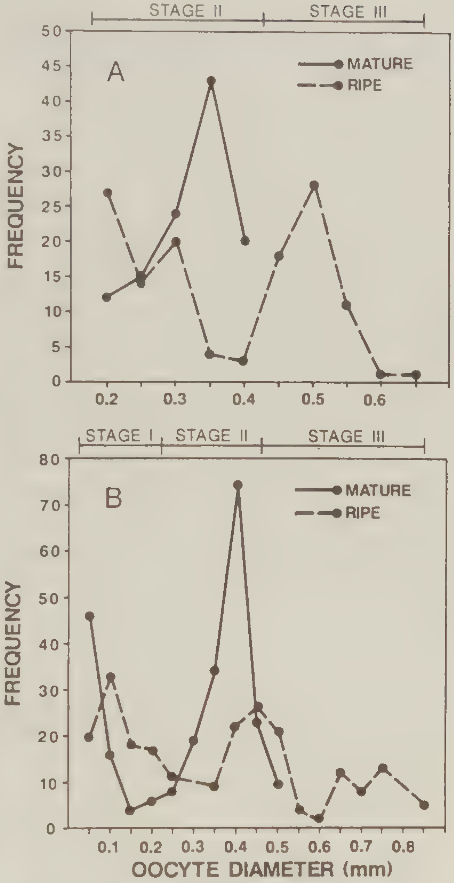


FIGURE 8.—Size-frequency distributions of uku ovaries in various stages of development (cf. Table 1) preserved in (A) Gilson's fluid and (B) Bouin's fluid. Each distribution shown represents a single ovary.

mode of immature oocytes not represented in the figure. Stage II ovaries contained a mode of oocytes at 0.30–0.35 mm, representing various stages of vitellogenesis, while stage III ovaries included this developing mode and another mode (0.50 mm) nearing hydration. A large amount of variation was noted in the relative frequency of oocytes in the most advanced mode of the stage III ovaries. Similar results were exhibited for size-frequency distributions of uku ovaries constructed by the cork borer method. This method allowed delineation of the immature mode as well as the other advanced stages (Fig. 8b). Additional evidence that multiple batches of oocytes ripen and are successively spawned was indicated by the wide range in GSI values calculated for both species during the spawning season.

Sex Ratio

The sex ratio of male to female uku was 1.05:1 (51.2% males, $N = 559$ individuals combined). A chi-square goodness of fit test suggested that this ratio was not significantly different from the expected 1:1 ratio ($\chi^2 = 0.302$, $P > 0.05$). By examining sex ratio at 50 mm FL intervals, independence was determined and the percentage of females was shown to decrease between the 600 and 750 mm FL categories from 50.0 to 40.9%, then increase 65.5% at 800 mm FL before reaching 100% beyond 900 mm FL. Based on two-way contingency table analysis, the percentage of females caught increased significantly towards the end of the spawning season (September–October; Table 3). Males were caught in higher percentages in the spawning months from May to July.

The sex ratio of male to female onaga differed significantly ($\chi^2 = 8.99$, $P < 0.05$) from 1:1 in favor of males (61.4%, $N = 347$ individuals combined). The overall ratio of males to females was 1.59:1. There was a significant preponderance of males within the 50 mm FL intervals from 600 to 750 mm. However, females predominated above 850 mm FL, reaching 100% of the individuals in the 950 mm FL category. The two-way contingency table analysis suggested that sex and month of capture were not independent (Table 3).

TABLE 3.—Tests of the hypothesis that sex ratio of uku and onaga did not vary significantly from the sample populations during the year. Data are pooled by 2 mo intervals for samples collected in 1984–87 (df = 5).

	Uku				Onaga		
Month	N		Percentage female	Contribution to total χ^2	N	Percentage female	Contribution to total χ^2
Jan.–Feb.	15	17			56	37.5	0.277
Mar.–Apr.	2		47.0	0.027	19	15.8	4.976
May–June	359		46.5	0.776	23	60.9	3.771
July–Aug.	88		43.0	1.637	76	47.4	1.292
Sept.–Oct.	69		63.8	6.153	130	33.9	2.719
Nov.–Dec.	28		64.3	2.673	62	41.9	0.174
Total				11.266*			13.209*

* = $P < 0.05$.

DISCUSSION

The spawning season for both uku and onaga extends throughout the summer months in Hawaii, as evidenced by the advanced condition of the ovaries and the peaks in ova diameters and GSI values during this period. This pattern has been reported in Hawaii for other snapper species, including *E. carbunculus* (Everson 1984) and *P. filamentosus* (Kikkawa 1984). Spawning activity also occurs during the austral summer for populations of *A. virescens* from New Caledonia (Fourmanoir and Laboute 1976) and East Africa (Talbot 1960; Nzioka 1979). Likewise, peak summer spawning with intermittent activity throughout the rest of the year seemed to be the pattern for *E. coruscans* in Vanuatu (Brouard and Grandperrin 1985). The seasonal peak in spawning activity may be most closely tied to increases in water temperature and day length, as suggested by Walsh (1987) who observed that spawning activity for Hawaiian reef fishes declined rapidly in September to October as maximum water temperatures were reached. This pattern would ensure optimum temperature conditions for developing larvae. A similar post-summer spawning decline associated with changing local environmental conditions was noted by Grimes and Huntsman (1980) for *Rhomboplites aurorubens* from North and South Carolina and by Everson (1984) for *E. carbunculus*. The extension of onaga's spawning season into November, with a peak in October, may reflect that the genus *Etelis* is restricted to much greater depths than are the other reef-associated lutjanid species. Seasonal changes in temperature and photoperiod are much less pronounced at these depths. In Vanuatu, Brouard and Grandperrin (1985) found that seasonal changes in gonad maturation based on GSI values differed among species inhabiting discrete depths.

Grimes (1987) has suggested two distinct spawning patterns for snappers. One is a restricted pattern with spawning centered around the summer months, typical of species associated with continental habitats where peaks in production cycles occur because of nutrient run-off resulting from high rainfall. The opposing pattern is characterized by year-round spawning with peaks occurring in spring and fall, a pattern thought to be typical of less productive insular populations. Grimes (1987) has noted that Cuba and New Caledonia are large islands that follow the continental pattern, with spawning peaks arising during periods of high rainfall. *Etelis carbunculus* (Everson 1984) and *P. filamentosus* (Kikkawa 1984) have also been reported to follow a restricted spawning pattern in the Northwestern Hawaiian Islands. Both uku and onaga in our study also followed the restricted spawning pattern associated with continental habitats. Spawning took place over a protracted period centered around the summer months. Neither species was found in spawning condition at any other time of the year. Since temporal primary production cycles exhibit little seasonal variation throughout the Hawaiian Archipelago (Bienfang and Szyper 1981; Bienfang et al. 1984), the basis for this restricted pattern observed for uku and onaga is unclear. Apparently, the seasonal changes in day length and water temperature in Hawaii provide adequate spawning stimuli.

Interspecies differences in size at sexual maturity also were noted. The slope of the logistic curve fitted to the size at sexual maturity data was considerably steeper for uku compared with onaga (Fig. 6). Uku matured at 450–500 mm FL, with nearly 100% mature above 550 mm FL, and onaga matured at 550–800 mm FL, with 100% mature at 850 mm FL. Size at sexual maturity differed between species in terms of the percentage of MAXLEN at which maturity occurred. Uku began maturing at about 429 mm FL or 42% of their MAXLEN, whereas onaga began maturing at about 522 mm FL or 54% of their MAXLEN. Talbot (1960) reported that male and female *A. virescens* of East Africa reached maturity at 410 mm SL (51%) and 465 mm SL (58%), respectively. *Aprion virescens* off Vanuatu matured at 440 mm FL, a figure that Brouard and Grandperrin (1985) calculated from a MAXLEN coefficient of 57.6%, which was based upon the average values obtained from 34 tropical fish species from the west coast of Africa. The same coefficient, applied to Vanuatu populations of *E. coruscans*, indicated that sexual maturity was reached at 470 mm FL, although developmental staging data obtained for this species revealed that mature fish were first sampled at 330–380 mm FL. The actual size at which maturity commenced in all of these locations agreed closely with our data for uku in Hawaii, while the percentage of MAXLEN values differed considerably. However, Hawaii and Vanuatu populations of onaga matured at substantially different sizes.

Disparities in size at sexual maturity between areas may reflect differences in resource utilization and growth allocation. Grimes (1987) calculated the average percentage of MAXLEN at which sexual maturity occurred for lutjanid populations occupying similar zoogeographic locations and habitats. Insular and continental populations had average MAXLEN values of 51 and 43%, respectively, while the deep (> 91 m) and shallow (< 91 m) species were calculated at 49 and 43%. The MAXLEN value of 42% calculated for the study population of uku indicates that this species fits the shallow, continental pattern. As previously mentioned, onaga are found at much greater depths and therefore seem to be less influenced by continental effects than uku. These observations are substantiated by the fact that the MAXLEN value of 54% calculated for onaga conforms closest to the deep, insular pattern reported in Grimes (1987). He reasoned that these anomalies may result from regional differences in food production. Fish from a relatively resource-rich environment may mature at a proportionally smaller size than fish in less productive habitats. He further speculated that selection may favor maturation at a larger maturing size in insular regions because the cost of year-round spawning may be higher in these areas.

Estimates of von Bertalanffy growth parameters, derived from weight-frequency distributions for uku and onaga landed in Hawaii in 1984–86, indicate that uku mature at about ages 4–5 (429 mm FL), while onaga begin maturing at ages 5–6 (522 mm FL) (Ralston and Kawamoto, fn. 1). In the same study, Ralston and Kawamoto (fn. 1) calculated the size at entry to the fishery as 650 mm FL for uku and 450 mm FL for onaga in the main Hawaiian Islands, indicating that, for onaga, the present fishery is capturing individuals that have not yet reached sexual maturity. Continuing this practice could lead to a serious decline in spawning stock biomass (Polovina 1987).

Sex ratio also differed between the two species. The ratio of male to female uku was judged not significantly different from the expected ratio of 1:1. In contrast, the onaga sex ratio was significantly different from unity in favor of males. Females dominated in the larger size classes for both species. The preponderance of large females has also been reported for other snapper species, including *Lutjanus synagris* (Reshetnikov and Claro 1976), *R. aurorubens* (Grimes and Huntsman 1980), and *E. carbunculus* (Everson 1984). This phenomenon is thought to be due to differential mortality of the sexes rather than to growth (Wenner 1972; Grimes and Huntsman 1980). The preponderance of male onaga in the smaller size ranges is more difficult to explain and may reflect intersexual behavioral differences. If smaller males feed more aggressively, they would be overly abundant in the catch. Differences in feeding behavior may also explain monthly variations in sex ratio reported for both species. The ratio of female uku increased markedly at the close of the spawning season, suggesting a heightened vulnerability to the fishing gear owing to what may be greater nutritional demands of postspawning females. Seasonally, the largest catch of uku occurs in summer (May–October), when fish are thought to form spawning aggregations (Ralston, fn. 2).

Numerous investigators have suggested that snappers are multiple spawners, based upon the presence of multiple size modes of developing oocytes (Min et al. 1977; Grimes and Huntsman 1980; Everson 1984; Kikkawa 1984; Grimes 1987). Other evidence reported as substantiating this phenomenon has been the wide variations exhibited in GSI's of *L. griseus* (Starck and Schroeder 1970) and *R. aurorubens* (Grimes and Huntsman 1980) during the spawning season. Ralston (1981) suggested that *P. filamentosus* is a multiple spawner because the ovaries of ripe females make up only about 4% of the total body weight, a relatively small percentage compared with that of a single spawning temperate species. These observations, the presence of multiple size modes of developing oocytes and the wide variations in GSI's, were noted for uku and onaga and suggested that these species also spawn repeatedly during the spawning season. Although it has been documented that the oocyte size-frequency distribution of many snapper species contains two or three distinct modes, the exact number of batches spawned per season is rarely reported. This is because the process of recruitment from the undifferentiated oocyte pool is dynamic and difficult to characterize (Grimes 1987).

Much of the above evidence is largely contingent on the assumption that multiple oocyte modes continue to develop and are successively spawned. Foucher and Beamish (1980) observed that, for Pacific hake, *Merluccius productus*, from the Strait of Georgia, oocyte development was multimodal during the spawning season, suggesting multiple spawning for this species. Histological examination of the ovaries revealed, however, that only the largest batch became hydrated and was spawned and all remaining residual yolked oocytes were resorbed. More direct evidence for this mode of spawning, as well as the delineation of the number of batches spawned, has been obtained through the process of identifying and ageing postovulatory follicles in species that exhibit these multiple modes of oocyte development. This method has been used to estimate spawning frequency in several engraulid species (Hunter and Goldberg 1980; Hunter and Macewicz 1980, 1985; Alheit et al. 1984; Parrish et al. 1986; Clarke 1987) and also for the skipjack tuna, *Katsuwonus pelamis* (Hunter et al. 1986). Ageing postovulatory follicles seems to work well for species normally found in large aggregations or schools but has yet to be applied to snappers. The ageing method using postovulatory follicles may be more difficult to apply to such species as snappers, which are known to occur in fewer numbers. Although our study attempted to identify postovulatory follicles in natural populations of uku and onaga, they could not be positively identified or aged. Future studies will have to address this problem, since the delineation of spawning frequency is important for accurate fecundity estimates.

ACKNOWLEDGMENTS

This study would not have been possible without the assistance of the staff at United Fishing Agency; Wing Sing, Inc.; Tropic Fish and Vegetable Center, Inc.; Fishland Market, Ltd.; Slow Poké Fishmarket; Star Markets, Ltd.; M. Q.

Fish Market; Nishimura Fish Market; Nobu's Fishmarket; and Hawaii Seafood Products, Inc. Special thanks go to the buyers who let us handle and measure their valuable fish, and who later supplied us with gonad samples. We would also like to thank reviewers S. Ralston, G. Boehlert, J. Uchiyama, C. Grimes, and S. Goldberg; all provided helpful suggestions. In addition, K. Kawamoto acted as auction liaison, and S. Ralston and D. Tagami provided invaluable statistical support. R. Shimojo provided many of the histological preparations.

LITERATURE CITED

Alheit, J., V. H. Alarcon, and B. J. Macewicz.
1984. Spawning frequency and sex ratio in the Peruvian anchovy, *Engraulis ringens*. Calif. Coop. Oceanic Fish. Invest. Rep. 25, p. 43–52.

Allen, G. R.
1985. FAO species catalogue. Snappers of the world. An annotated and illustrated catalogue of lutjanid species known to date. FAO Fish. Synop. 125, Vol. 6, 208 p. + colored plates.

Amesbury, S. S., and R. F. Myers.
1982. Guide to the coastal resources of Guam, volume I. The fishes. Univ. Guam Mar. Lab. Contrib. 173, 141 p.

Bagenal, T. B., and E. Braum.
1968. Eggs and early life history. *In* W. E. Ricker (editor), IBP handbook No. 3, methods for assessment of fish production in fresh waters, p. 159–181. Blackwell Scientific Publ., Oxford and Edinburgh.

Bienfang, P. K., and J. P. Szyper.
1981. Phytoplankton dynamics in the subtropical Pacific Ocean off Hawaii. Deep-Sea Res. 28A(9): 981–1000.

Bienfang, P. K., J. P. Szyper, M. Y. Okamoto, and E. K. Noda.
1984. Temporal and spatial variability of phytoplankton in a subtropical ecosystem. Limnol. Oceanogr. 29:527–539.

Brouard, F., and R. Grandperrin.
1985. Deep-bottom fishes of the outer reef slope in Vanuatu. South Pacific Commission, Seventeenth Regional Technical Meeting on Fisheries, Noumea, New Caledonia, 5–9 August 1985. SPC/Fisheries 17/WP.12, 126 p.

Clarke, T. A.
1987. Fecundity and spawning frequency of the Hawaiian anchovy or nehu, *Encrasicholina purpurea*. Fish. Bull., U.S. 85:127–138.

Crossland, J.
1977. Seasonal reproductive cycle of snapper *Chrysophrys auratus* (Forster) in the Hauraki Gulf. N.Z. J. Mar. Freshwater Res. 11:37–60.

Druzhinin, A. D.
1970. The range and biology of snappers (Fam. Lutjanidae). J. Ichthyol. 10:717–736.

Everson, A. R.
1984. Spawning and gonadal maturation of the ehu, *Etelis carbunculus*, in the Northwestern Hawaiian Islands. *In* R. W. Grigg and K. Y. Tanoue (editors), Proceedings of the Second Symposium on Resource Investigations in the Northwestern Hawaiian Islands, Vol. 2, May 25–27, 1983, University of Hawaii, Honolulu, Hawaii, p. 128–148. UNIHI-SEAGRANT-MR-84-01.

Foucher, R. P., and R. J. Beamish.
1980. Production of nonviable oocytes by Pacific hake (*Merluccius productus*). Can. J. Fish. Aquat. Sci. 37:41–48.

Fourmanoir, P., and P. Laboute.
1976. Poissons de Nouvelle-Calédonie et des Nouvelles Hébrides. Les éditions du Pacifique, Papeete, Tahiti, 376 p.

Grimes, C. B.
1987. Reproductive biology of the Lutjanidae: A review. *In* J. J. Polovina and S. Ralston (editors), Tropical snappers and groupers: Biology and fisheries management, p. 239–294. Westview Press, Boulder.

Grimes, C. B., and G. R. Huntsman.
1980. Reproductive biology of the vermilion snapper, *Rhomboplites aurorubens*, from North Carolina and South Carolina. Fish. Bull., U.S. 78:137–146.

Gunderson, D. R., P. Callahan, and B. Goiney.
1980. Maturation and fecundity of four species of *Sebastes*. Mar. Fish. Rev. 42(3-4): 74–79.

Hilge, V.
1977. On the determination of the stages of gonad ripeness in female bony fishes. Meeresforchung 25(1976/77):149–155.

Hunter, J. R., and S. R. Goldberg.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:641–652.

Hunter, J. R., and B. J. Macewicz.
1980. Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning for the northern anchovy, *Engraulis mordax*, during the 1979 spawning season. Calif. Coop. Oceanic Fish. Invest. Rep. 21:139–149.
1985. Measurement of spawning frequency in multiple spawning fishes. *In* R. Lasker (editor), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*, p. 79–94. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36.

Hunter, J. R., B. J. Macewicz, and J. R. Sibert.
1986. The spawning frequency of skipjack tuna, *Katsuwonus pelamis*, from the South Pacific. Fish. Bull., U.S. 84:895–903.

Kikkawa, B. S.
1984. Maturation, spawning, and fecundity of opakapaka, *Pristipomoides filamentosus*, in the Northwestern Hawaiian Islands. *In* R. W. Grigg and K. Y. Tanoue (editors), Proceedings of the Second Symposium on Resource Investigations in the Northwestern Hawaiian Islands, Vol. 2, May 25–27, 1983, University of Hawaii, Honolulu, Hawaii, p. 149–160. UNIHI-SEAGRANT-MR-84-01.

Kikkawa, B. S., and A. R. Everson.
1984. Gonadal maturation, fecundity, and spawning of the greater amberjack, *Seriola dumerili* (Risso), in Hawaiian waters with references to ciguatoxin incidences. *In* R. W. Grigg and K. Y. Tanoue (editors), Proceedings of the Second Symposium on Resource Investigations in the Northwestern Hawaiian Islands,

Vol. 2, May 25–27, 1983, University of Hawaii, Honolulu, Hawaii, p. 161–178. UNIHI-SEAGRANT-MR-84-01.

Masuda, H., C. Araga, and T. Yoshino.
1975. Coastal fishes of southern Japan. [In Jpn.] Tokai Univ. Press, Tokyo, 379 p.

Min, T. S., T. Senta, and S. Supongpan.
1977. Fisheries biology of *Pristipomoides* spp. (Family Lutjanidae) in the South China Sea and its adjacent waters. Singapore J. Primary Ind. 5(2):96–115.

Ni, I-H., and E. J. Sandeman.
1984. Size at maturity for northwest Atlantic redfishes (*Sebastes*). Can. J. Fish. Aquat. Sci. 41:1753–1762.

Nzioka, R. M.
1979. Observations on the spawning seasons of East African reef fishes. J. Fish Biol. 14:329–342.

Parrish, R. H., D. L. Mallicoate, and R. A. Klingbeil.
1986. Age dependent fecundity, number of spawnings per year, sex ratio, and maturation stages in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 84:503–517.

Polovina, J. J.
1987. Assessment and management of deepwater bottom fishes in Hawaii and the Marianas. *In* J. J. Polovina and S. Ralston (editors), Tropical snappers and groupers: Biology and fisheries management, p. 505–532. Westview Press, Boulder.

Pooley, S. G.
1987. Demand considerations in fisheries management—Hawaii's market for bottom fish. *In* J. J. Polovina and S. Ralston (editors), Tropical snappers and groupers: Biology and fisheries management, p. 605–638. Westview Press, Boulder.

Ralston, S.
1981. A study of the Hawaiian deepsea handline fishery with special reference to the population dynamics of opakapaka, *Pristipomoides filamentosus* (Pisces: Lutjanidae). Ph.D. Thesis, Univ. Washington, Seattle, 204 p.

Reshetnikov, Yu. S., and R. M. Claro.
1976. Cycles of biological processes in tropical fishes with reference to *Lutjanus synagris*. J. Ichthyol. 16:711–723.

Snedecor, G. W., and W. G. Cochran.
1978. Statistical methods. 6th ed. Iowa State Univ. Press, Ames, IA, 593 p.

Starck, W, A., II, and R. E. Schroeder.
1970. Investigations on the gray snapper, *Lutjanus griseus*. Stud. Trop. Oceanogr. (Miami) 10, 224 p. (Copyright 1971).

Talbot, F. H.
1960. Notes on the biology of the Lutjanidae (Pisces) of the East African coast, with special reference to *L. bohar* (Forskal). Ann. S. Afr. Mus. 45:549–573.

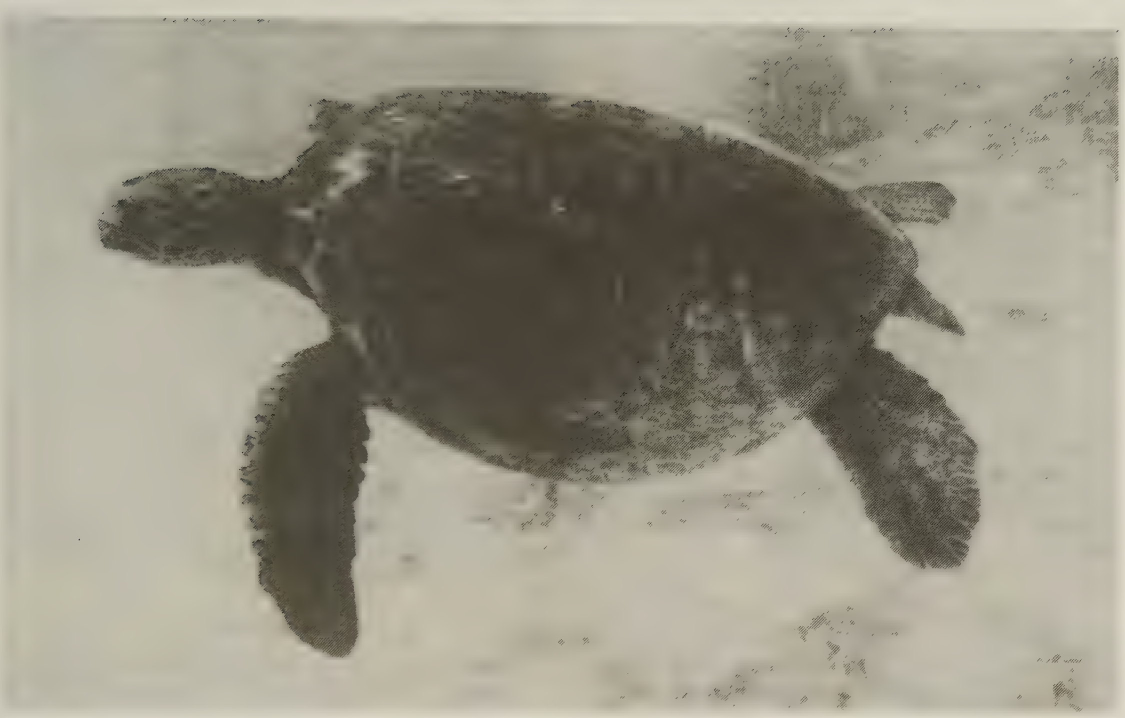
Van Dalsen, A. P.
1977. An improved technique for subsampling eggs for fecundity studies. Fish. Bull., S. Afr. 9:6–10.

Wallace, R. A., and K. Selman.
1981. Cellular and dynamic aspects of oocyte growth in teleosts. Am. Zool. 21:325–343.

Walsh, W. J.
1987. Patterns of recruitment and spawning in Hawaiian reef fishes. Environ. Biol. Fishes 18:257–276.

Wenner, A. M.
1972. Sex ratio as a fuction of size in marine crustacea. Am. Nat. 106:321–350.

Western Pacific Regional Fishery Management Council.
1986. Combined fishery management plan, environmental assessment and regulatory impact review for the bottomfish and seamount groundfish fisheries of the western Pacific region. Western Pacific Regional Fishery Management Council, 1164 Bishop Street, Honolulu, HI 96813, var. pag.



GREEN TURTLE, *Chelonia mydas*

Robert G. Forsyth, George H. Balazs

NOMENCLATURE/TAXONOMY

Scientific name . . . *Chelonia mydas* (Linnaeus) 1758
Preferred common name . . . . . Green turtle
Other common names . . . Hawaii--Honu; Tonga--Fonu, Fonu Tu'a'uli, Fonu Tu'akula, Fonu Tu'apolata, Tuai Fonu; Society Islands--French: Tortue, Tahitian: Honu; Guam--hagan, kame; Western Samoa--lau-ei; Tokelau--fonu; Fiji--vonu damu, vonu loa, mako loa, ika damu
Class . . . . Reptilia
Order . . . . Testudinata
Family . . . . Cheloniidae

GEOGRAPHIC RANGE

Chelonia mydas can be found in all tropical and temperate seas between lat. 35°N and 35°S and in waters remaining above 20°C in the coldest month of the year (King 1982). Although the green turtle is a circumglobal species, it should not be regarded as a single interbreeding assemblage, but as discrete populations genetically isolated from each other (Groombridge 1982).

Major worldwide nesting sites for green turtles include beaches on the Pacific and Caribbean coasts of Mexico; the Galápagos Islands off Ecuador; the Caribbean coast of Costa Rica; the South American coasts of Surinam, Guyana, and French Guiana; Ascension Island and the Cape Verde Islands in the mid-Atlantic; in the Indian Ocean on the coast of South Yemen; and the east coast of Saudi Arabia as well as several islands in the Persian Gulf. Europa Island in the Mozambique Channel is an important nesting colony, and in Africa, there is nesting in Somalia, Tanzania, and Mozambique. Both coasts of Thailand and Malaysia, especially the offshore islands, still have large numbers of nestings (Pritchard 1979).

Green turtles nest and reside throughout the vast Pacific Ocean region (Figure 1). Most nestings today are on small uninhabited islands or remote beaches which are not readily accessible and have not been overexploited by man (Figure 2). Some of the more important nesting areas are Raine Island, Pandora Cay, and the Capricorn Bunker Group, Australia (Limpus and Fleay 1983); the Manus District of Papua New Guinea (Spring 1982a); d'Entrecasteaux Reef in New Caledonia (Pritchard 1982); Scilly Island in the Society Islands; Rose Atoll in American Samoa (Hirth 1971); Canton Island in the Phoenix Group (Balazs 1975); and French Frigate Shoals (Figure 3) in the Northwestern Hawaiian Islands (NWHI) (Balazs 1982c).

REASON FOR INCLUSION IN SERIES

Green turtles and their eggs are an important food source for many coastal and island villagers throughout the Pacific Ocean region. They also play an important part in religious and ceremonial practices in some cultures, although far more so in former times (Johannes 1986). Until recently, the green turtle was important commercially; historically, it played a major role in the European exploration and settlement of the Western Hemisphere and parts of Asia by supplying large amounts of protein that could be easily stored (alive) on ships (Pritchard 1979).

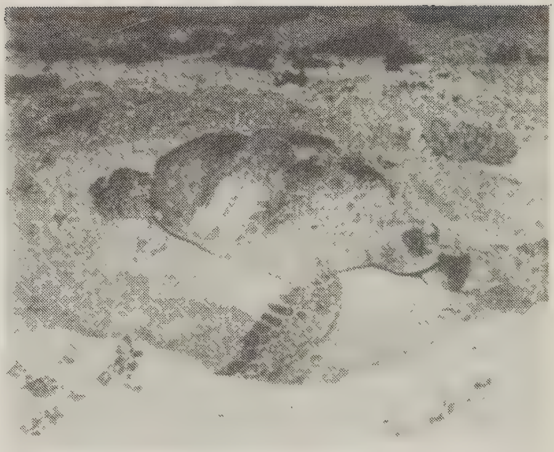


Figure 1. Nesting green turtle. Painted number is for short-term resighting during the nesting season. East Island, FFS, NWHI.

Except for stable populations in Australia, the green turtle populations in the Pacific are currently in jeopardy. They are listed as endangered by the International Union for Conservation of Nature and Natural Resources (IUCN). They also are listed in the U.S. Endangered Species Act and in Appendix 1 of the Convention on International Trade in Endangered Species of Wild Fauna and Flora. (France, Italy, Japan, and Surinam have entered reservations for the Appendix 1 listing (Groombridge 1982),

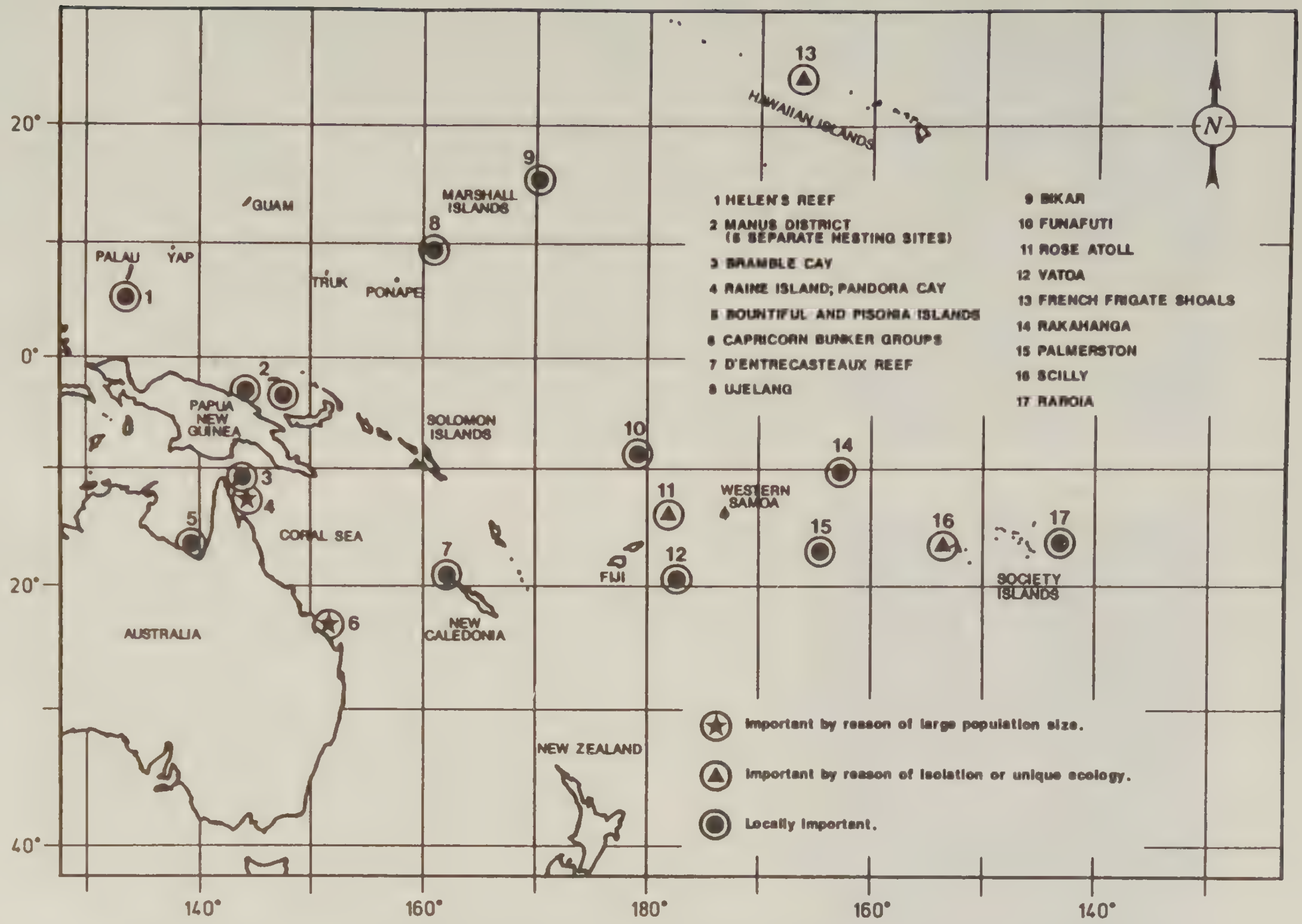


Figure 2. Distribution of notable nesting sites of green turtles in the Pacific Ocean region.

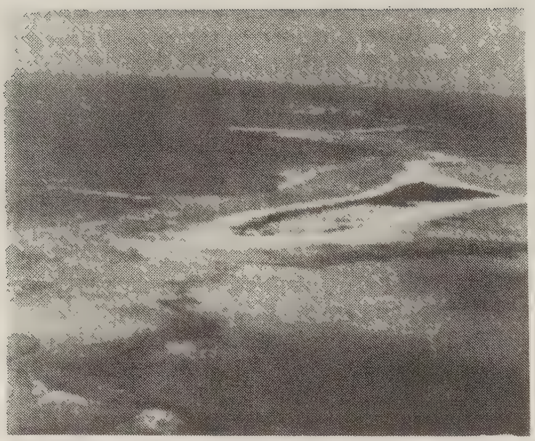


Figure 3. Aerial view of East Island at FFS in the NWHI. Largest green turtle nesting colony in the Hawaiian Islands.

but Japan recently withdrew this option.)

MORPHOLOGY AND IDENTIFICATION AIDS

The green turtle is the largest of the hard-shelled marine turtles, measuring up to 125 cm in carapace length and 230 kg. Its carapace is heart shaped and smooth; its body is very streamlined for efficient movement through the water. The head is relatively small and anteriorly rounded. The front flippers are long, and the normal mode of progression both in the water and on land involves simultaneous sweeps of the forelimbs.

The normal carapace scute pattern for the green turtle includes an anterior nuchal (precentral) scute, 5 median vertebral (central) scutes, with 4 pairs of costal (lateral) scutes, 11 pairs of marginal scutes, and 1 pair of supracaudal (postcentral) scutes (see front cover photo). It is not uncommon to have variations in scute numbers.

Coloration of the carapace is a dark blue black as a hatchling, changing to a pattern of radiating streaks of buff, gold, brown, and black in juveniles. This pattern is variable even for turtles of the same size and population. As an adult, coloration shows somewhat less variability with background colors of green, olive, brown, buff, or black.

The plastral scutes of the green turtle from front to rear consist of a single intergular followed by the paired gular, humeral, pectoral, abdominal, femoral, and anal, ending with a single postanal. The plastron is connected to the carapace by four pairs of inframarginal scutes. The coloration is white in hatchlings, turning to a pale yellow or orange as the turtles mature. Hawaiian green turtle hatchlings go through a radical color change in the plastron pigmentation that has not been reported in other populations. At 5.8-cm carapace length (2 weeks old), the plastron becomes diffused with black and gray pigment. This intensifies until hatchlings reach 7 to 8 cm in carapace length (4 weeks old) (Figure 4). Thereafter, it fades away, usually disappearing completely by 13 cm or less (20 weeks old). Free-ranging turtles presumably undergo these same changes; however, because posthatchlings have not been observed during their pelagic stage, this has not been verified (Balazs 1986b).

The head scalation typically includes a large frontoparietal scale on the crown, preceded by a smaller frontal and a single pair of elongate prefrontals. On each side of the frontal is a supraocular, followed by four postocular scales. Behind the

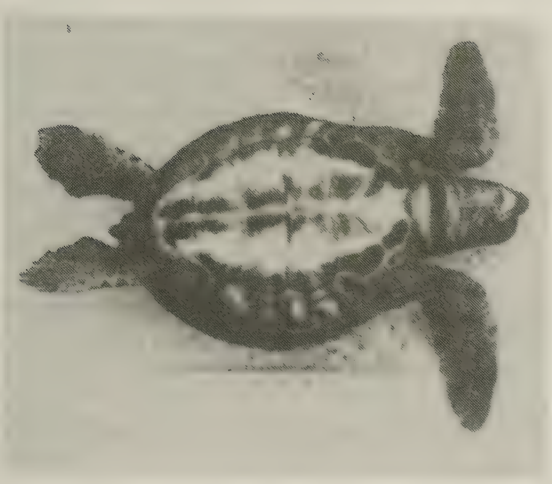


Figure 4. Four-week-old Hawaiian green turtle showing dark pigmentation phase of plastron.

supraocular is a temporal, and situated behind the frontoparietal is a pair of parietals with an additional temporal on the outer margins of each parietal.

Sex is externally indeterminate before the onset of maturity. Females are a minimum of 80-cm straight-line carapace length at maturity; males are slightly smaller. At or just before maturity, the tail of the male elongates and thickens at the base. The tail of the male reaches a short distance beyond its hind flippers, whereas the female's tail barely extends beyond the posterior end of the carapace.

LIFE HISTORY

Mating

Courtship and copulation take place in shallow water in the general vicinity of the nesting beaches. Most copulations occur early in the mating season, and females do not copulate after laying their first clutch of eggs (Balazs 1980b). There is some uncertainty as to when fertilization actually takes place. Some researchers believe that fertilization is delayed until the following nesting season. This hypothesis raises the question of when the eggs of virgin females are fertilized, as well as the process by which spermatozoa would be stored for 2, 3, or at least 4 years between nestings. Most authorities now believe that fertilization is of the current season's eggs. This would still require the short-term storage of spermatozoa because most green turtles lay multiple clutches of eggs (Ehrhart 1982).

Reproductive Cycle

Adult females that remigrate to nesting beaches tend to do so on 2-, 3-, or 4-year cycles or longer. However, low recovery rates of remigrating females suggest that many females may nest only once in their lifetime. A 21-year study involving 12,000 tagged females at Tortuguero showed only a 16.4% remigration rate (Hughes 1982). High tag loss may account for this low number, but high mortality from fishing pressure and other impacts is certainly a possibility.

Nesting

Nesting normally takes place throughout the summer months (seasons reverse for the Southern and Northern Hemispheres) in the Pacific islands, with strong seasonal peaks that vary with location. Nesting occurs at night on sandy beaches above the high watermark. Once the female locates a suitable area to deposit her eggs, she digs a body pit by using her foreflippers in a strong sweeping motion and throwing the sand behind her. This process lowers the whole turtle 9 to 18 in. Once this is completed, she digs out the flask-shaped egg cavity by using her hind flippers in alternating actions. Once the cavity is finished, oviposition commences (Pritchard 1979). The number of eggs deposited can vary widely, but the average is between 100 and 110. Oviposition normally takes 20 to 30 min (Balazs 1980b). On completion, the egg chamber is filled in with the hind flippers. Then with the foreflippers, the turtle fills in the body pit, leaving a pit in front of the actual nest.

Most females nest more than once a season. At East Island in the NWHI, as many as six egg clutches from a single female have been recorded. The mean, however, is 1.8 clutches. Time between nestings at East Island ranges from 11 to 18 days, with a mean of 13 days (Balazs 1980b). These numbers are generally consistent with data collected at other Pacific islands.

Research shows that green turtles have strong site fixity in nesting. Remigrating females return to the same nesting beach time after time. The possibility exists that hatchlings are somehow imprinted so that they return to the same beach once they reach maturity (Hirth 1971). Owens et al. (1982) have described an alternate explanation, termed "social facilitation model." In this hypothesis, first-time nesters encounter and follow experienced adults to the nesting beach, which they "learn" by olfactory and other navigation systems.

Eggs

Green turtle eggs are spherical and white. Most eggs are covered with mucous when they leave the cloaca (Hirth 1971). Average diameter and weight for eggs at East Island (NWHI) are 44 mm and 50 g, respectively. Incubation ranges from 54 to 88 days, with a mean of 64.5 days (Balazs 1980b). Egg size varies slightly from one population to another.

The excavation of 40 nests after emergence at East Island (NWHI) showed that 88.5% of the eggs were fertilized and that fertility of eggs tended to decrease slightly in later clutches (Balazs 1980b).

Sea turtle eggs do not hatch when incubated outside the temperature range of 24° to 34°C. Also, the higher the temperature, the shorter the incubation period is (Limpus et al. 1983). Incubation temperatures also have been shown to affect sexual differentiation. Even a change of 1° or 2°C can affect the sex ratio; lower temperatures result in a higher percentage of males, whereas higher temperatures yield more females (Mrosovsky and Yntema 1982).

Hatchlings

It usually takes 3 to 7 days for Chelonia hatchlings to break free from their eggs and dig to the surface. Movement to the surface is a joint effort bringing the hatchlings up as one or two groups. If high (greater than 33°C) sand temperatures are encountered near the surface, they cease activity and wait for nightfall and lower sand temperatures. The hatchlings emerge at night, usually a few hours after sunset, and, once oriented, move quickly toward the beach. Emerging at night eliminates exposure to hot sand surfaces that could be lethal or inhibiting and also eliminates exposure to diurnal terrestrial and marine predators (Hirth

1971). Once hatchlings enter the water, they swim vigorously out to sea. At this time, all contact is lost with the hatchlings until they reappear as juveniles in coastal feeding grounds.

Longevity

Little is known about the natural lifespan of C. mydas. Two captive Hawaiian green turtles, sent to Canada in 1956 as juveniles and later returned to Sea Life Park on Oahu, are still alive after 32 years (Balazs 1983a). Tag recoveries of 12 turtles (4 females and 8 males) originally tagged as adults in Hawaii exceed 9 years, and at Tortuguero in Costa Rica, 1 tagged nesting female has been resighted over a 19-year period (Balazs 1980b). This information suggests that green turtles are relatively long-lived.

Work has been initiated by Zug and Balazs (1985) in using a skeletochronological technique in aging green turtles. Estimates of age are being made through observations of the cyclic marks of skeletal growth in humeri of Chelonia. Early results suggest slow growth and late maturity for turtles in Hawaii. The two oldest turtles aged in this work were estimated to be 135 and 81 years old. This technique was used by Zug et al. (1986), with apparent success in aging loggerhead turtles, Caretta caretta.

Basking

In a few remote areas of the Pacific, green turtles have the habit of coming ashore to bask (Figure 5). The only areas where this behavior has been well documented are the Gulf of Carpentaria and North West Cape in Australia, the Galápagos Islands, and the NWHI. In Australia, only females bask and then only during the breeding season, possibly to escape overzealous males. Basking in the Galápagos Islands has not been observed now for several years and may no longer be a behavioral characteristic of the population. Basking is still common for Chelonia in the NWHI and has been documented on all island groups in the chain (Balazs 1980b; Kam 1986) (Figure 6).

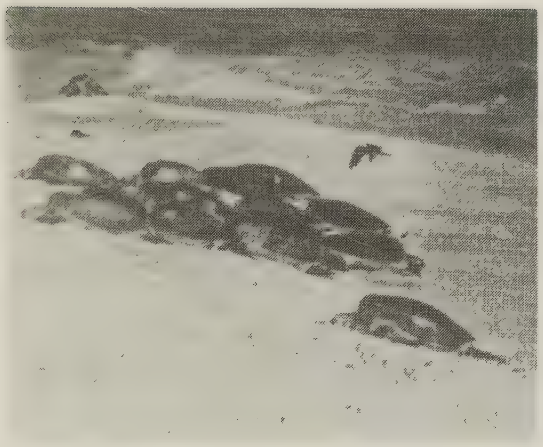


Figure 5. Basking green turtles at East Island, FFS, NWHI.

Basking normally takes place during the day, but it is not uncommon for turtles to also haul out in the late evening and "bask" into the night (Balazs 1980b; Forsyth et al. 1988). Observations of basking green turtles at French Frigate Shoals (NWHI) revealed that relatively cool beaches are selected for basking, major time is not invested in basking behavior, and an increase in body temperature from solar radiation appears to limit the time they stay ashore (Whittow and Balazs 1982).

The current hypotheses for basking behavior include thermoregulation,

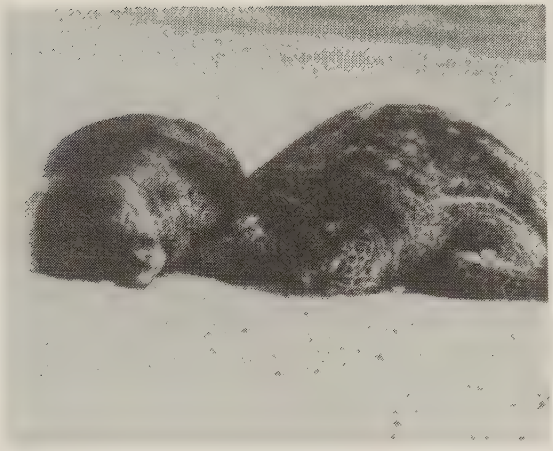


Figure 6. Basking green turtle with Hawaiian monk seal. East Island, FFS, NWHI.

aiding ecdysis, freeing the turtle of ectoparasites or eliminating epizoic algae, aiding in the synthesis of vitamin D, facilitating social behavior, and avoiding predators (Hirth 1971; Balazs 1980b). Garnett et al. (1985) believe that energy conservation may be the principal purpose for basking behavior in Australia.

Migration and Navigation

Green turtles periodically migrate between foraging and nesting beaches. Low recovery rates of tagged turtles have made it difficult to establish migratory routes, and modes of navigation are still unknown (Hirth 1971). Tag recoveries have shown that turtles will migrate from foraging areas to nesting beaches even when "suitable" nesting sites are available locally (Meylan 1982b).

Figure 7 shows documented migrations of green turtles in the Pacific (Balazs 1982b). Relatively few turtles have been tagged in the Pacific Basin; nevertheless, some of the longest recoveries recorded are from this area. The recovery in New Caledonia of green turtles tagged at Scilly Island in the Society Islands indicated that turtles migrate in excess of 4,000 km (Meylan 1982b).

Migratory speeds calculated from tag return data show most turtles can travel 20 to 40 km a day, even when going against the prevailing currents. These calculations are from turtles traveling long distances and are minimum averages made with the assumption that turtles are captured immediately after arrival at the capture site (Meylan 1982b).

The current hypotheses of turtle navigation include bicoordinate celestial navigation, light-compass sense, olfactory cues, perception of Coriolis force, magnetic sense, inertial guidance, sonar sense, subtle oceanographic cues such as currents and wave patterns, and perhaps a composite of several of these factors (Hirth 1971).

GROWTH CHARACTERISTICS

When the hatchling emerges from the nest, it weighs approximately 30 g and has a straight-line carapace length just over 5 cm. At this time, the turtle "disappears" and does not "reappear" until it reaches a size of 35 cm or more. Generally referred to as "lost years," this is a time when the turtle is living in a pelagic environment. Since there have been no observations of turtles during this period, their diet is unknown but assumed to be small invertebrates and fish eggs. Hawaiian Chelonia raised in captivity from hatchlings required at least 19 months to reach a straight-line carapace length of 35 cm. These

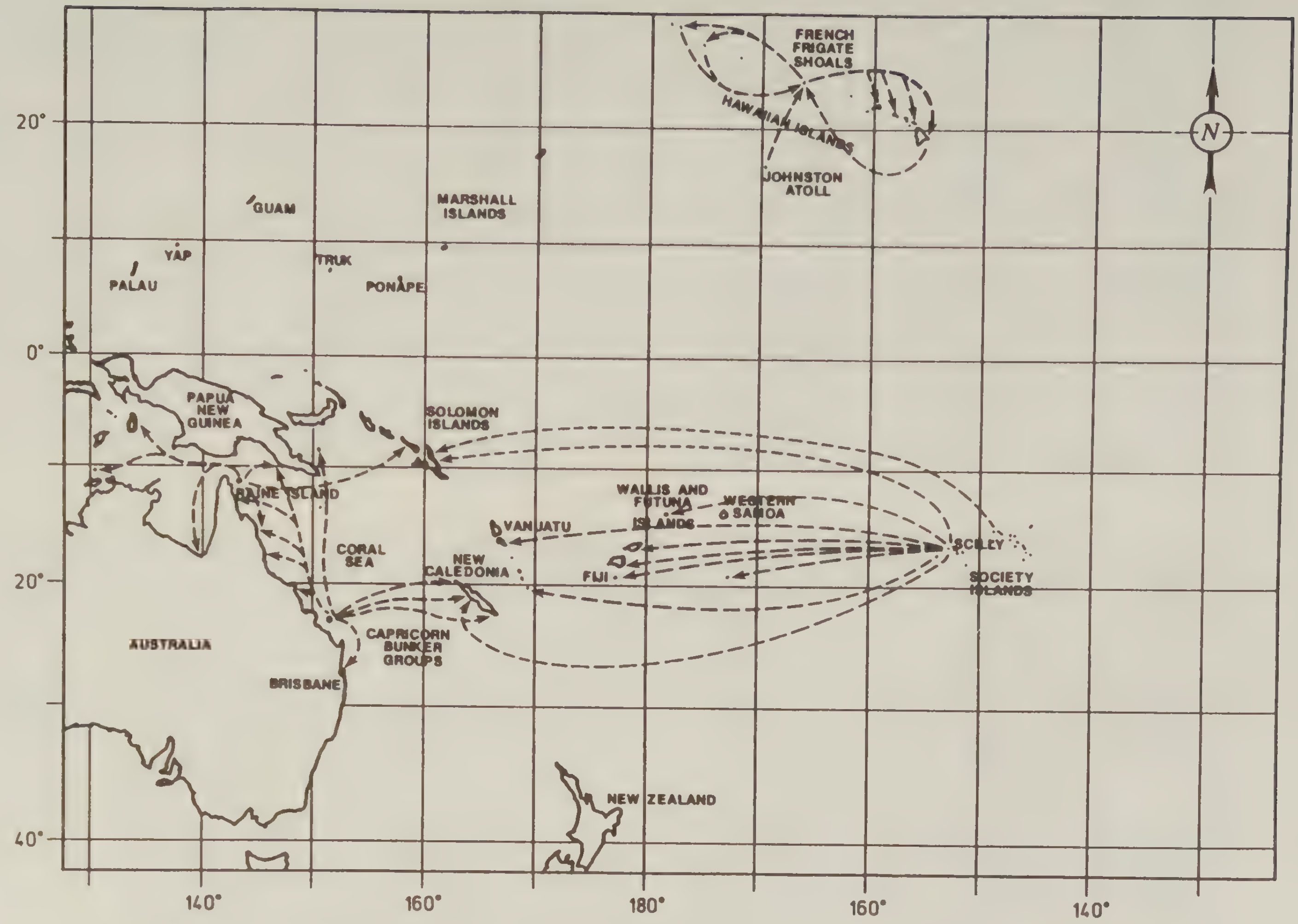


Figure 7. Migrations of green turtles in the Pacific Ocean region, as shown by recaptures of tagged individuals. Arrows do not necessarily show routes of travel.

turtles were fed a diet of pelleted dry food, fresh frozen squid, and fish (Balazs 1980b). Once the juveniles reach a size of 35 to 40 cm, they begin to appear in coastal areas and start a herbivorous existence.

Growth information is obtained by tagging and recapturing turtles in their natural environment. In a study of growth rates of immature green turtles undertaken by Balazs (1982a) in the Hawaiian Archipelago, growth rates varied from area to area, but within one area, growth rates were consistent even though turtle sizes varied. The most rapid rates of growth were recorded for turtles foraging extensively on Pterocladia capillacea. This study included seven study sites ranging from the Kau District on the Island of Hawaii (lat. 19°08'N, long. 155°30'W) to Kure Atoll (lat. 28°25'N, long. 178°10'W) at the opposite end of the archipelago. Extrapolating from rates in this study, it would take a 35-cm turtle in the Kau District 8.7 years to reach sexual maturity (81 cm is the minimum size at which nesting takes place in Hawaii) and 47.9 years for a 35-cm turtle at Kure Atoll (the slowest growth rate in the archipelago). These estimates assume that long-range migrations to other foraging areas are not made. All 69 turtles recaptured in this study were found in the same area where they were originally tagged. The recapture intervals ranged from 2 to 37 months. This shows a tendency towards long-term residency, backed by the fact that generally a full size range of turtles can be found at these foraging sites (Balazs 1982a).

Independent studies in Australia (Limpus 1979; Limpus and Walter 1980) and Great Inagua, Bahamas (Bjorndal and Bolten 1988), also showed much slower growth rates than previously estimated for this species. Bjorndal and Bolten (1988) concluded that green turtle growth is dependent on the quality of the diet and that these data will allow the use of growth rates in different areas to assess the quality of the habitat.

Once green turtles reach maturity, growth rates decline (Carr and Carr 1970). Most growth data on adults are gathered at nesting beaches when females come ashore to deposit their eggs. The size range of nesting females in Hawaii is 80.8 to 106.2 cm straight-line carapace length, with a mean of 92 cm (Balazs 1980b). This wide range, coupled with slow growth rates after reaching maturity, leads some researchers to believe that turtles are maturing at different sizes.

FISHERY

The importance of green turtles as a fishery varies throughout the Pacific. In Hawaii and other areas under U.S. jurisdiction in the Pacific, green turtles are listed as threatened under the Endangered Species Act and cannot be legally taken. In Australia, turtles can be taken by indigenous people and then only for subsistence (Limpus and Fleay 1983). In most other areas in the Pacific, turtles can still be legally harvested with some restrictions.

Traditional methods of capturing turtles include netting with large-diameter mesh net, harpooning with either a fixed or detachable spear tip, by hand, and the taking of nesting females (Spring 1982b; Johannes 1986). Today, Pacific islanders use high-speed boats with outboard engines to hunt green turtles. They have easy access to areas that before could be reached only with difficulty and then only at certain times of the year. They use scuba gear and spear guns to take turtles. In Palau, they attach polypropylene rope to the butt of the spear gun. The other end of the rope is attached to a combination float and fish-stringer. When a large turtle is shot, they release the spear gun, wait for the prey to tire, then retrieve it once the float resurfaces. This practice also occurs in Yap (Johannes 1986).

Most turtles today are caught by the inhabitants of coral atolls and coastal villages, some still depending on the turtle for subsistence. Even so, concern does exist for the future of the turtle in the Pacific. Older villagers are beginning to notice a decline in the number of turtles. The emergence of a "money economy" and gradual breakdown of traditional taboos coupled with the advantages of modern equipment are impacting the turtle (McCoy 1982; Spring 1982b). There is no way to really tell how many turtles are being caught and to what degree the population may be threatened by overhunting.

Chelonia eggs are also collected by the local inhabitants of the islands and coastal areas of the Pacific. Nesting beaches in many areas have been designated as "off limits" because of the dwindling number of nesting turtles and eggs. In Australia, eggs are collected by the indigenous people, but compared with exploitation of turtles, egg collection appears to have little impact on wild populations (Kowarsky 1982). In Tokelau on the islands of Fakaofo and Nukunonu, whenever a clutch of eggs is found, it is dug up, whereas Atafu has a ban on the taking of eggs, except for a few that are allowed to be removed from each nest (Balazs 1983b). In Palau, laws regarding the harvesting of turtles and their eggs are respected by only a few fishermen (Johannes 1986).

In 1979, the South Pacific Commission and the National Marine Fisheries Service (Southwest Fisheries Center Honolulu Laboratory) jointly held a workshop in Noumea, New Caledonia, to address the problems facing marine turtles in the tropical Pacific islands. Turtle experts from the United States, Australia, and the Pacific islands gathered to discuss and make recommendations that would help secure turtle populations of the region for island people. These recommendations included providing increased protection to sea turtles and their preferred habitats (South Pacific Commission 1980).

ECOLOGICAL ROLE

Food

Green turtles are primarily herbivores but will eat animal matter opportunistically (Table 1). They will eat jellyfish when these are abundant (Limpus 1978) and, on a few occasions, have been reported to eat fish eggs (Fritts 1981). Captive turtles are normally fed a diet of fish and/or squid. Information on food sources is obtained by (1) direct feeding observations, (2) analysis of stomach contents of dead turtles, (3) recovery of incompletely digested food in fecal pellets, and (4) sampling of stomach contents of live turtles by using a flexible plastic tube (Balazs 1980a).

Behavior in Foraging Pastures

Green turtles approximately 35 cm or more in length spend most of their

Table 1. Some important food sources recorded for green turtles in the Pacific Ocean region.

Locality	Principal food source
Main Hawaiian Islands	*Pterocladia capillacea*, *Amansia glomerata*, *Acanthophora spicifera*, *Halophila hawaiiana*, *Codium edule*, *C. arabicum*, *C. phasmaticum*, *Ulva fasciata*, *U. reticulata*, *Ahnfeltia concinna*
Northwestern Hawaiian Islands	*Caulerpa racemosa*, *Codium arabicum*, *C. phasmaticum*, *C. edule*, *Ulva fasciata*, *Turbinaria ornata*, *Spyridia filamentosa*
Johnston Atoll	*Caulerpa racemosa*, *Bryopsis pennata*, *Halophila ovalis*
Tonga	*Halodule ovalis*, *Halophila* sp., *Syringodium isoetifolium*
Tokelau	*Valonia aegagropila*, *Turbinaria ornata*
Fiji	*Halodule pinifolia*, *H. ovalis*, *Syringodium isoetifolium*
Kermadec Islands	*Pterocladia capillacea*
Tahiti	Algae
Palau	Seagrass
Truk	Seagrass and algae
Torres Strait, Australia	Red and green algae
Papua New Guinea	Seagrass
Southern Great Barrier Reef, Australia	*Chlorodesmis* sp., *Turbinaria* sp., *Amansia* sp., *Enteromorpha* sp., *Polysiphonia* sp., *Champia* sp., *Dictyota* sp., *Zostera* sp., *Thalasia* sp.

lives living in coastal waters where adequate amounts of preferred benthic algae or seagrasses are present. Algae and seagrasses are restricted to shallow depths where sunlight, substrate, and nutrients are conducive to plant growth. Feeding pastures are normally less than 10 m deep and frequently not more than 3 m (Balazs 1980b).

Feeding strategy varies depending on the habitat characteristics. Turtles observed feeding in rough surf usually take only a single rapid breath before returning to the bottom. In more protected areas, turtles have been observed spending as much as 2 min on the surface, taking three to eight deep breaths before diving (Balazs 1980b). Active turtles surface every 30 sec to 15 min.

Green turtles "sleep" in the general vicinity of feeding pastures, often in water between 20 and 50 m deep. Their preferences are coral recesses and undersides of ledges with sandy bottoms that are relatively free of strong currents. Resting turtles with small radio transmitters were found to have bottom times of up to 2.5 h (Balazs 1980b; Balazs et al. 1987).

Predation

Eggs--Nonhuman predation of eggs is minimal at most nesting beaches in the Pacific Ocean region. Small mammals such as mongooses, feral pigs, and feral dogs are the most effective egg predators, easily locating turtle nests probably by using olfactory cues (Stancyk 1982). However, most extant green turtle nesting occurs on remote uninhabited islands, thereby avoiding effective mammal predation.

Hatchlings--Ghost crabs and hermit crabs are the most widespread land predators but probably take no more than 5% of the hatchlings. However, hatchlings at nesting beaches infested with rats, feral cats, and mongooses have very high mortality. Most researchers believe that, once the hatchlings enter the water, predation by small sharks and reef fishes is quite high; however, it is difficult to assess the impact once the hatchlings enter the marine environment. In a survey conducted near East Island (NWHI) during peak hatching months in 1974, 101 ulua, *Caranx ignoblis* and *C. melampygus*; 16 wrasses, *Thalassoma purpureum* and *Bodianus bilunulatus*; and 13 gray reef sharks, *Carcharhinus amblyrhynchos*, were captured. Stomach contents were checked for hatchlings, but no evidence of hatchling predation was found (Balazs 1980b).

Juveniles, Subadults, and Adults--The tiger shark, *Galeocerdo cuvieri*, is the most commonly observed predator of juvenile, subadult, and adult *Chelonia* (Stancyk 1982). Intensive shark eradication programs in the main Hawaiian Islands show tiger sharks regularly feeding on turtles. A single shark at Pearl and Hermes Reef (NWHI) accounted for five turtles ranging from an estimated 53 to 64 cm in carapace length (Balazs 1980b). Other large species of shark are known to feed on green turtles, and juveniles have been found in the stomachs of large groupers.

Parasites, Symbionts, and Diseases

Known ectoparasites of green turtles include the burrowing barnacle, *Stephanolepas muricata*; the piscicolid leech, *Ozobranchus branchiatus*; and the talitroidean amphipod, Hyachelia tortugae. Symbionts include the barnacles, Chelonibia testudinata and Platylepas hexastylos; and the remora, Echeneis sp. (Balazs 1980b).

A number of internal parasites, especially Spirorchidae, have been identified from green turtles in the Pacific. These may well be of significance to the well-being and survival status of the turtle (Glazebrook et al. 1981; Blair 1986, 1987).

Neoplastic growths identified as fibropapillomas (tumors) are being seen on a growing number of green turtles in Hawaii (Balazs 1986a). The cause of these growths is still unknown, but possible causes include immune response to trematode ova, secretion of hirudin by marine leeches, viruses, excessive solar radiation, chemical pollutants that impair the immune system, stress, and a genetic predisposition to neoplasm. These growths range in size from small warts to huge masses 30 cm in diameter and are usually found around the neck, flippers, tail, and eyes. They can result in reduced vision, disorientation, blindness, and physical obstruction to normal swimming and feeding. It is believed that in almost all instances, death ultimately results (Balazs 1986a). An increase in the incidence of fibropapillomas in the Hawaiian population, which has also been seen in Florida green turtles, has prompted members of the Hawaiian Sea Turtle Recovery Team to give high priority to the investigation of incidence, impact, and cause of fibropapillomas (Hawaiian Sea Turtle Recovery Team 1989).

ENVIRONMENTAL REQUIREMENTS

Beaches

Green turtles nest on a variety of beach types. Nesting requirements include (1) easy accessibility from the sea, (2) a beach platform high enough that it is not inundated by spring tides or flooded by the water table below, and (3) beach sand that facilitates gas diffusion but is moist enough and fine enough to prevent excessive slippage during construction of the nest (Mortimer 1982).

Human activity and development of beach front property can have a negative impact on turtle nesting beaches. Artificial lighting is the most obvious deterrent. Females are known to shun beaches that have artificial lighting (Mortimer 1982; Coston-Clements and Hoss 1983), and hatchlings are easily disoriented by bright lights which can cause substantial unnatural mortality from crawling hopelessly inland away from the sea. (Limpus and Fleay 1983; Raymond 1984). Physical barriers such as jetties, groins, seawalls, and retaining walls may limit access, excluding turtles from prime nesting habitat. Increased levels of human activity in developed areas appear to discourage females from nesting (Witham 1982).

Internesting Habitat

Study of habitat occupied between nestings within a breeding season has received little attention to date, despite its importance. Large numbers of reproductive turtles may be concentrated in relatively small areas, making them vulnerable to impact by commercial harvesting, incidental catch, or ecological disasters such as oil spills. It is important to define

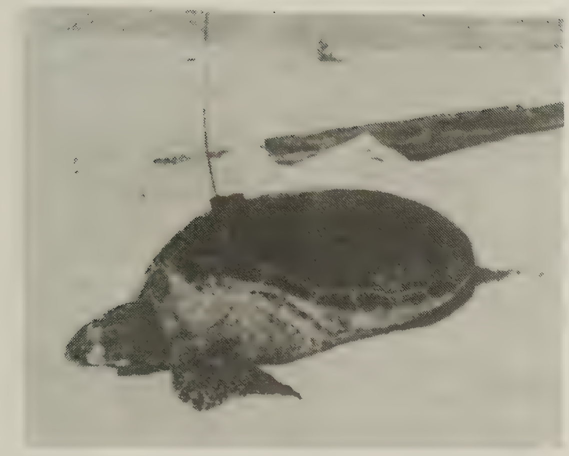


Figure 8. Adult green turtle with radio transmitter attached to carapace (see Dizon and Balazs 1982). Trig Island, FFS, NWHI.

these internesting areas and give them appropriate protection (Meylan 1982a).

Radio tracking of eight green turtles (four males, four females) at French Frigate Shoals (NWHI) during the breeding season showed strong site fixity for males and females alike (Figure 8). All eight turtles stayed in proximity of the nesting islands where transmitters were attached, even though another important nesting island was only 9 km away (Dizon and Balazs 1982).

Foraging Pastures

Green turtles are unique among sea turtles in being primarily herbivores. They are mainly associated with seagrass pastures or areas abundant in desirable marine algae (Hirth 1971). Research in Hawaii on feeding and resting habitats is the most thorough to date in the Pacific islands. Green turtles in Hawaii can be found wherever adequate accessible food sources and resting habitat are available. The nearshore benthic habitat surrounding the main Hawaiian Islands is limited by dramatic drop-offs usually within a few kilometers of the shore. Algae, the main food source in Hawaii, is found in the nearshore waters where sunlight and proper substrate are conducive to growth. Freshwater seepage stimulates algal growth in many areas, which are often popular feeding spots. Most habitat is hard-bottom surface or coral rubble that is required by their major food sources for proper attachment. One important turtle foraging area, however, on the south coast of Molokai has extensive mud flats where seagrass, _Halophila_ _hawaiiana_, is present (Balazs et al. 1987).

At Johnston Island, a remote atoll located south of the main Hawaiian islands, green turtles use two feeding areas that exist side by side. On the south shore is a large field of _Caulerpa_ that extends 100 m. Slightly seaward, in deeper water, _Bryopsis_ is present on the tops of coral heads. Both areas will normally have several foraging turtles that can easily be monitored from a nearby peninsula. Johnston Island is of special ecological interest with regard to environmental contamination because of its use as a storage area for nerve gas, mustard gas, and dioxin. High altitude nuclear testing also took place here in 1958 and 1962 (Balazs 1985b; Balazs and Forsyth 1986).

Resting habitat is found in proximity to foraging areas, usually within 2 km or less. Large turtles prefer small caves or protective outcroppings often associated with submarine cliffs. These usually have fine-grained sand or powdery silt bottoms that the turtles rest on. In Hawaii, these sites are found along an

18- to 27-m drop-off around much of the coastline. Smaller turtles can be found resting closer to shore at the base of coral heads, in crevices, or vertical-walled channels within the reef flat. These areas must protect the turtles from large waves and strong currents (Balazs 1980b).

Pelagic

Posthatchlings are now believed to spend their first years as epipelagic dwellers in borders of currents and eddies. Young turtles swimming seaward eventually encounter convergences that are created by advection and downwelling. These convergences occur more often and last longer than originally thought, making the migrations of young turtles more feasible than originally supposed. The same advection forces that draw in the young turtles also draw in the macroplankton that they feed on. This pelagic stage is longer than originally thought, with current estimates in excess of 3 years (Carr 1987).

Marine debris, which was considered only an aesthetic problem by a 1973 U.S. National Academy of Sciences workshop on ocean pollution, has become a major environmental problem. The dumping of large amounts of plastic into the marine environment has changed the composition and extent of marine debris, affecting marine animals, especially seabirds and turtles (Shomura in press). During the pelagic period, young turtles are being exposed to this ever-increasing amount of debris. The debris is accumulated in the same convergences used by the turtles which are prone to eating plastic scraps and other debris. The number of turtles washing up dead from impaction of the alimentary canal with plastics or from entanglement indicates marine debris may be a major threat to sea turtle survival (Carr 1987). The impact on sea turtles from ingesting or becoming entangled in synthetic marine debris has been extensively documented by Balazs (1985a).

LITERATURE CITED

Balazs, G.H. 1975. Marine turtles in the Phoenix Islands. Atoll Res. Bull. 184:1-7.

Balazs, G.H. 1980a. Field methods for sampling the dietary components of green turtles, *Chelonia mydas*. Herpetol. Rev. 11:5-6.

Balazs, G.H. 1980b. Synopsis of biological data on the green turtle in the Hawaiian Islands. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-7, 141 pp.

Balazs, G.H. 1982a. Growth rates of immature green turtles in the Hawaiian Archipelago. Pages 117-125 *in* K.A. Bjorndal, ed. Biology and Conservation of Sea Turtles. Smithsonian Institution Press, Wash., D.C.

Balazs, G.H. 1982b. Sea turtles: A shared resource of the Pacific islands. South Pac. Comm. Fish. Newsl. 232:22-24.

Balazs, G.H. 1982c. Status of sea turtles in the central Pacific. Pages 243-252 *in* K.A. Bjorndal, ed. Biology and Conservation of Sea Turtles. Smithsonian Institution Press, Wash., D.C.

Balazs, G.H. 1983a. Hawaiian turtles in Canada. Kilo i'a (Waikiki Aquarium Newsl.) 39:1-3.

Balazs, G.H. 1983b. Sea turtles and their traditional usage in Tokelau. Atoll Res. Bull. 279:1-29.

Balazs, G.H. 1985a. Impact of ocean debris in marine turtles: Entanglement and ingestion. Pages 387-429 *in* R.S. Shomura and H.O. Yoshida, eds. Proceedings of the workshop on the fate and impact of marine debris, 26-29 November 1984, Honolulu, Hawaii. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-54.

Balazs, G.H. 1985b. Status and ecology of marine turtles at Johnston Atoll. Atoll Res. Bull. 285:1-46.

Balazs, G.H. 1986a. Fibropapillomas in Hawaiian green turtles. Mar. Turtle Newsl. 39:1-3.

Balazs, G.H. 1986b. Ontogenetic changes in the plastron pigmentation of hatchling Hawaiian green turtles. J. Herpetol. 20:280-282.

Balazs, G.H., and R.G. Forsyth. 1986. Status and ecology of marine turtles at Johnston Atoll: 1985 assessment. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396. Southwest Fish. Cent. Admin. Rep. H-86-9, 22 pp.

Balazs, G.H., R.G. Forsyth, and A.K.H. Kam. 1987. Preliminary assessment of habitat utilization by Hawaiian green turtles in their resident foraging pastures. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-71, 107 pp.

Bjorndal, K.A., and A.B. Bolten. 1988. Growth rates of immature green turtles, Chelonia mydas, on feeding grounds in the southern Bahamas. Copeia 1988:555-564.

Blair, D. 1986. A revision of the subfamily Microscaphidiinae (Platyhelminthes: Digenea: Microscaphidiidae) parasitic in marine turtles (Reptilia: Chelonia). Aust. J. Zool. 34:241-277.

Blair, D. 1987. A revision of the subfamily Octangiinae (Platyhelminthes: Digenea: Microscaphidiidae) parasitic in marine turtles (Reptilia: Chelonia). Aust. J. Zool. 35:75-92.

Carr, A. 1987. Impact of nondegradable marine debris on the ecology and survival outlook of sea turtles. Mar. Pollut. Bull. 18(6B):352-356.

Carr, A., and M.H. Carr. 1970. Recruitment and remigration in a green turtle nesting colony. Biol. Conserv. 2:282-284.

Coston-Clements, L., and D.E. Hoss. 1983. Synopsis of data on the impact of habitat alteration on sea turtles around the southeastern United States. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-SEFC-117, 57 pp.

Dizon, A.E., and G.H. Balazs. 1982. Radio telemetry of Hawaiian green turtles at their breeding colony. Mar. Fish. Rev. 44(5):13-20.

Ehrhart, L.M. 1982. A review of sea turtle reproduction. Pages 29-38 in K.A. Bjorndal, ed. Biology and Conservation of Sea Turtles. Smithsonian Institution Press, Wash., D.C.

Forsyth, R.G., D.J. Alcorn, T. Gerrodette, and W.G. Gilmartin. 1988. The Hawaiian monk seal and green turtle on Pearl and Hermes Reef, 1986. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-107, 24 pp.

Fritts, T.H. 1981. Pelagic feeding habits of turtles in the eastern Pacific. Mar. Turtle Newsl. 7:4-5.

Garnett, S.J., G. M. Crowley, and N. Goudberg. 1985. Observations of non-nesting emergence by green turtles in the Gulf of Carpentaria. Copeia 1985:262-264.

Glazebrook, J.S., R.S.F. Campbell, and D. Blair. 1981. Pathological changes associated with cardiovascular trematodes (Digenea: Spirorchidae) in a green sea turtle Chelonia mydas. J. Comp. Path. 91:361-368.

Groombridge, B. (compiler). 1982. The IUCN Amphibia-Reptilia red data book, art 1. Green turtle. IUCN (Int. Union Conserv. Nat. Nat. Resour.), pp. 151-180.

Hawaiian Sea Turtle Recovery Team. 1989. Final draft recovery plan for Hawaiian sea turtles. 95 pp.

Hirth, H.F. 1971. Synopsis of biological data on the green turtle Chelonia mydas (Linnaeus) 1758. FAO Fish. Synop. 85:1-8, 19.

Hughes, G.R. 1982. Nesting cycles in sea turtles--typical or atypical? Pages 81-89 in K.A. Bjorndal, ed. Biology and conservation of sea turtles. Smithsonian Institution Press, Wash., D.C.

Johannes, R.E. 1986. A review of information on the subsistence use of green and hawksbill sea turtles on islands under United States jurisdiction in the western Pacific Ocean. Southwest Region, Natl. Mar. Fish. Serv., NOAA, Terminal Is., CA 90731-7415. Southwest Region Admin. Rep. SWR-86-2, 41 pp.

Kam, A.K.H. 1986. The green turtle, Chelonia mydas, at Laysan Island, Lisianski Island, and Pearl and Hermes Reef, summer 1982. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-107, 24 pp.

King, F.W. 1982. Historical review of the decline of the green turtle and the hawksbill. Pages 183-188 in K.A. Bjorndal, ed. Biology and Conservation of Sea Turtles. Smithsonian Institution Press, Wash., D.C.

Kowarsky, J. 1982. Subsistence hunting of sea turtles in Australia. Pages 305-313 in K.A. Bjorndal, ed. Biology and Conservation of Sea Turtles. Smithsonian Institution Press, Wash., D.C.

Limpus, C. 1978. The reef. Pages 187-222 in H.J. Lavery, ed. Exploration North, Australia's Wildlife from Desert to Reef. Richmond Hill Press, Victoria, Australia.

Limpus, C. 1979. Notes on growth rates of wild turtles. Mar. Turtle Newsl. 10:3-5.

Limpus, C.J., and A. Fleay. 1983. Management and turtles. Pages 535-540 in J.T. Baker, R.M. Carter, P.W. Sammarco, and K.P. Stark, eds. Proceedings: Inaugural Great Barrier Reef Conference, Townsville, August 28-September 2, 1983. JCU Press.

Limpus, C.J., P. Reed, and J.D. Miller. 1983. Islands and turtles. The influence of choice of nesting beach on sex ratio. Pages 397-402 in J.T. Baker, R.M. Carter, P.W. Sammarco, and K.P. Stark, eds. Proceedings: Inaugural Great Barrier Reef Conference, Townsville, August 28-September 2, 1983. JCU Press.

Limpus, C.J., and D.G. Walter. 1980. The growth of immature green turtles (Chelonia mydas) under natural conditions. Herpetologica 36:162-165.

McCoy, M.A. 1982. Subsistence hunting of turtles in the western Pacific: The Caroline Islands. Pages 275-280 in K.A. Bjorndal, ed. Biology and Conservation of Sea turtles. Smithsonian Institution Press, Wash., D.C.

Meylan, A. 1982a. Behavioral ecology of the west Caribbean green turtle (Chelonia mydas) in the internesting habitat. Pages 67-80 in K.A. Bjorndal, ed. Biology and Conservation of Sea Turtles. Smithsonian Institution Press, Wash., D.C.

Meylan, A. 1982b. Sea turtle migration--evidence from tag returns. Pages 91-100 in K.A. Bjorndal, ed. Biology and Conservation of Sea Turtles. Smithsonian Institution Press, Wash., D.C.

Mortimer, J.A. 1982. Factors influencing beach selection by nesting sea turtles. Pages 45-51 in K.A. Bjorndal, ed. Biology and Conservation of Sea Turtles. Smithsonian Institution Press, Wash., D.C.

Mrosovsky, N., and C.L. Yntema. 1982. Temperature dependence of sexual differentiation in sea turtles: Implications for conservation practices. Pages 59-65 in K.A. Bjorndal, ed. Biology and Conservation of Sea Turtles. Smithsonian Institution Press, Wash., D.C.

Owens, D.W., M.A. Grassman and J.R. Henderson. 1982. The imprinting hypothesis and sea turtle reproduction. Hepetologica 38:124-135.

Pritchard, P.C.H. 1979. Encyclopedia of Turtles. T.F.H. Publication Inc., Neptune, NJ, 895 pp.

Pritchard, P.C.H. 1982. Marine turtles of the South Pacific. Pages 253-262 in K.A. Bjorndal, ed. Biology and Conservation of Sea Turtles. Smithsonian Institution Press, Wash., D.C.

Raymond, P.W. 1984. Sea turtle hatchling disorientation and artificial beachfront lighting: A review of the problem and potential solutions. Center for Environmental Education, Wash., D.C., 72 pp.

Shomura, R.S. In press. Impact of marine debris in the tropical Pacific. Mar. Pollut. Bull.

South Pacific Commission. 1980. Joint SPC/NMFS workshop on marine turtles in the tropical Pacific islands: Report of meeting. Noumea, New Caledonia, 11-14 December, 16 pp.

Spring, C.S. 1982a. Status of marine turtle populations in Papua New Guinea. Pages 281-289 in K.A. Bjorndal, ed. Biology and Conservation of Sea Turtles. Smithsonian Institution Press, Wash., D.C.

Spring, C.S. 1982b. Subsistence hunting of marine turtles in Papua New Guinea. Pages 291-295 in K.A. Bjorndal, ed. Biology and Conservation of Sea Turtles. Smithsonian Institution Press, Wash., D.C.

Stancyk, S.E. 1982. Non-human predators of sea turtles and their control. Pages 139-152 in K.A. Bjorndal, ed. Biology and Conservation of Sea Turtles. Smithsonian Institution Press, Wash., D.C.

Whittow, G.C., and G.H. Balazs. 1982. Basking behavior of the green turtle (Chelonia mydas). Pac. Sci. 36:129-139.

Witham, R. 1982. Disruption of sea turtle habitat with emphasis on human influence. Pages 519-522 in K.A. Bjorndal, ed. Biology and Conservation of Sea Turtles. Smithsonian Institution Press, Wash., D.C.

Zug, G.R., and G.H. Balazs. 1985. Skeletochronological age estimates for Hawaiian green turtles. Mar. Turtle Newsl. 33:9-10.

Zug, G.R., A.H. Wynn, and C. Ruckdeschel. 1986. Age determination of loggerhead sea turtles, Caretta caretta, by incremental growth marks in the skeleton. Smithson. Contrib. Zool. 427, 34 pp.

8921

Exp Biol (1989) 48: 89–94

Experimental Biology
© Springer-Verlag 1989

O_2 tension, swimming-velocity, and thermal effects on the metabolic rate of the Pacific albacore *Thunnus alalunga*

Jeffrey B. Graham[1], **William R. Lowell**[1], **N. Chin Lai**[1], **and R. Michael Laurs**[2]

[1] Physiological Research Laboratory and Marine Biology Research Division, Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA 92093, USA
[2] National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA 92093, USA

Summary. The oxygen consumption rates ($\dot{V}O_2$) of 9 albacore tuna, *Thunnus alalunga* (8.5–12 kg) were measured at sea in a swimming respirometer to determine the effects of relative swimming velocity, ambient O_2 tension, and water temperature. Significant positive relationships were obtained between tail-beat frequency and relative speed and between relative speed and $\dot{V}O_2$. The albacore metabolic rate was not appreciably affected by exposure to water temperatures ranging from 13.5° to 16.9°C. Brief exposure to hyperoxia (200–400 mmHg), which was done to reduce the initial stress upon fish in the respirometer, did not affect $\dot{V}O_2$. Hypoxia (50–99 mmHg), however, did tend to reduce $\dot{V}O_2$ and affect swimming velocity.

Key words: *Thunnus alalunga* – Tuna – Oxygen consumption – Swimming metabolism

Introduction

The strength and metabolic requirements of tunas pose logistically difficult problems for in vivo and respirometry studies. However, the last few years have witnessed steady progress toward the objective of maintaining tunas in viable condition while controlled physiological experiments are carried out. Recent studies have examined aspects of the acid-base physiology (Perry et al. 1985a, b) and the blood gas parameters (Jones et al. 1986) of swimming skipjack. A major contribution to the study of tuna physiology has been made by the United States National Oceanographic and Atmospheric Administration's R.V. *David Starr Jordan* which, between 1977 and 1985, was used for physiological, behavioural, and ecological studies on the Pacific albacore *Thunnus alalunga* (Bonnaterre).

Physiological studies with the albacore have demonstrated that it has a large blood volume (Laurs et al. 1978), thermoregulates in cool water (Graham and Dickson 1981), has a metabolic rate close to that of a mammal (Graham and Laurs 1982), exhibits a reversed temperature effect for haemoglobin-O_2 binding that is in turn integrated with its elevated body temperature (Cech et al. 1984; White et al. 1988), and has a high blood pressure and cardiac output, as well as a negative pericardial pressure (Breisch et al. 1983; Lai et al. 1987; White et al. 1988).

The first metabolic measurements reported for *T. alalunga* (Graham and Laurs 1982) were made at sea with a respirometer that did not have elaborate thermal, ambient O_2, or water velocity control capabilities. In studies carried out aboard the *Jordan* in 1985 an improved water tunnel design was used, and we report here on the combined and separate effects of water O_2 tension, temperature, and swimming velocity, as well as the influence of the time since capture on the O_2 consumption rate ($\dot{V}O_2$) of the Pacific albacore. Such studies will improve our understanding of albacore physiology, and reveal environmental factors that are likely to determine the short-term movement patterns of migrating schools. This in turn may lead to the more efficient harvest and management of this important fishery species.

Materials and methods

Studies were carried out in August 1985, using albacore collected off Monterey, California (USA) were sea surface temperatures ranged from 15.8° to 17.0°C. Fish were caught by

---

Offprint requests to: J. B. Graham

trolling and handled as described by Graham and Laurs (1982), Lai et al. (1987) and White et al. (1988). Fish not seriously injured by the hook were quickly transferred to the chilled (about 15°C), oxygenated, and flowing water in a 470 l swimming respirometer.

The respirometer, similar to the water channel described by Prange (1976), consisted of a closed loop of flowing water, separated horizontally, and connected at each end by curved metal vanes. The respirometer working section (113 × 30 × 29 cm) was contained in the upper horizontal channel. A lucite cover containing a removable hatch was sealed over the upper channel and working section by a neoprene gasket. The hatch was opened to introduce and remove the fish. A standpipe was used to add water. This pipe and bent tubes in each corner of the top were used to purge air from the chamber.

Water was driven around the system by a three quarter hp variable speed motor (Minarik Blue Chip II) mounted outside the lower channel, and coupled to the propeller shaft which entered the respirometer through sealed bearings. Honeycomb collimator material, at both ends of the working section, confined the fish and smoothed the flow. Rectilinear flow through the working section was verified by observation of moving particles. The maximum velocity of the respirometer in this configuration is about 1.25 m/s. Velocities were calibrated by a flow meter (General Oceanics, Model 2035-mk III). Because of the solid blocking effects induced by the cross-sectional area of the fish body, working section velocities were corrected as described by Graham and Laurs (1982).

To control temperature and maintain clean water during tests, respirometer water was pumped through a heat-exchanging and filtration circuit. Prior to most studies, respirometer water was chilled to 14°–15°C, which is within the range normally encountered by albacore swimming below the mixed layer (Laurs and Lynn 1977; Laurs et al. 1980). Tanks of compressed O_2 were used to elevate respirometer O_2 tension. Earlier studies (Graham and Dickson 1981; Graham and Laurs 1982) suggested that this relieved stress, and enabled albacore to recover more quickly from the shocks of capture and handling, and adjust to confinement in the respirometer.

A Yellow Springs O_2 and temperature meter (Model 54A) and probe (5450/5750) were used to monitor temperature and O_2tension in the respirometer. The O_2 electrode had been standardized with air and N_2 gas, and was regularly calibrated in air during the tests. A voltage-controlled reciprocating pump circulated respirometer water from the system, through the probe housing and back again.

A fish was placed in the system, and observed prior to respirometry measurements to verify that it swam regularly. The anterior third of the working section was painted black in order to calm the fish, and provide orientation marks for maintaining station, and the front end of the section was always covered with a black cloth during swimming studies. Depending upon fish performance and condition, the total time that fish were maintained in the respirometer ranged from 177 to 553 min. The time interval that passed before respirometry began, varied between 14 and 119 min. Two to eight replicate $\dot{V}O_2$ measurements were made on each albacore. For this, the respirometer was sealed for a specific time, and the decline in PO_2 recorded. Then the system was opened, the O_2 level raised, and the process repeated. During each run the water velocity was continuously adjusted so that the fish swam steadily. In addition to O_2, temperature, and velocity, fish tail-beat frequency was recorded at regular intervals during each run. After tests were completed the fish was removed and its mass and fork length (L) determined. The final fish tested (no. 11) was in such excellent condition at the end of the tests that it was released.

Calculations of $\dot{V}O_2$ were based on the net (background corrected) reduction rate of ambient O_2. Data were reduced to mean instantaneous $\dot{V}O_2$ estimates, based on small increments of PO_2 change, and the mean values of other recorded variables over the same period. These were then delineated, for interfish comparison, on the basis of temperature (± 1°C) and PO_2 range (either ± 100 or ± 50 mmHg) in the respirometer, relative swimming speed (L/s), and tail-beat frequency (Hz). All regression equations were tested for a significant ($P < 0.05$) slope by *t*-test.

Results and Discussion

Data were obtained for 9 albacore (8.5–12.0 kg) swimming at various combinations of temperature (13.5°–18.0°C), O_2 tensions (ranging from 50–440 mmHg, normoxia = 150 mmHg) and speed (0.5–1.4 L/s). Our experimental protocol and the form of data acquisition are illustrated for albacore no. 8 which was used in 3 $\dot{V}O_2$ runs (Table 1). Run 1 began after a 79 min habituation period, and the fish swam in the respirometer for 6.1 h. All runs began in high ambient PO_2 which decreased with time. Table 1 indicates that the performance of fish no. 8 improved with time since capture. At first this fish would not swim and for most of the first 3 h, it swam irregularly and had a low $\dot{V}O_2$. By the third run, both its $\dot{V}O_2$ and velocity were elevated. Tables 2 and 3 contain summary data for albacore nos. 5 and 11. These tables have the same format as Table 1, except that $\dot{V}O_2$ is reported for the entire run rather than smaller PO_2 regimes. As with fish no. 8, albacore nos. 5 and 11 also seemed to gain strength with time. This may be a "training" effect, or may indicate the fishes' recovery from the rigours of capture and handling.

It was found that differences in fish body size and physiological state following capture, often established a narrow range of swimming speeds; pooled data for all fish in all combinations of PO_2 range, temperature, and speed (Fig. 1) demonstrate this. Fig. 1A shows the significant linear relationship between tail-beat frequency and relative velocity determined for all fish under all experimental conditions. Inspection of these data, however, reveals that tail-beat frequencies for the lowest PO_2 range (dots, Fig. 1A) occur consistently at higher velocities, suggesting that low PO_2 – possibly by affecting caudal amplitude – alters the relationship between albacore tail-beat frequency and swimming speed. The ratio of speed to tail-beat (stride length) for albacore (0.5–0.6) is similar to that of other scombrids over this velocity range (Magnuson 1978). The significant relationship between swimming velocity and $\dot{V}O_2$ (Fig. 1B) is not affected by high PO_2. It can be seen, however, that

Table 1. Records of mean water temperature, tail-beat frequency, swimming speed, and instantaneous $\dot{V}O_2$ of albacore no. 8 (11.0 kg) during 3 respirometry runs. Note that respirometer PO_2 declines during each run. Time intervals indicate duration of each run and the time before and between each run. Total elapsed test time was 6.1 h

		Run 1						Run 2						Run 3			
		79 min	104 min					27 min	71 min				38 min	49 min			
PO_2			400 −300	299 −200	199 −150	149 −100	99 −50		400 −300	299 −200	199 −150	149 −100		400 −300	299 −200	199 −150	149 −100
°C	$\bar{x}$		14.6 ±0.1	14.1 ±0	14.1 ±0.1	14.7 ±0	14.7 ±0		15.0 ±0	14.9 ±0	14.8 ±0	14.8 ±0		15.2 ±0	15.2 ±0	15.2 ±0	15.2 ±0
	n		10	15	8	10	8		7	21	7	9		7	10	4	3
Tail beat[a]	$\bar{x}$		1.86	1.91	1.92	1.93	1.94		2.28	2.17	2.11	2.11		2.37	2.14	2.17	2.14
(Hz)	n		8	11	7	5	6		6	5	6	8		4	7	2	3
U[b] (L/s)	$\bar{x}$		0.74	0.93	1.01	1.11	1.19		1.10	1.11	1.15	1.23		1.00	1.06	1.11	1.11
	n		10	15	8	10	8		7	21	7	9		7	4	4	3
$\dot{V}O_2$ (ml/min)	$\bar{x}$		57.0 ±15	37.9 ±3	39.3 ±4	37.5 ±3	43.1 ±8		56.0 ±5	68.9 ±16	52.4 ±5	41.6 ±7		63.9 ±3	66.3 ±1	65.3 ±1	66.6 ±5
	n		10	15	8	10	8		6	17	7	8		6	10	4	3

[a] All SE value <0.1
[b] All SE values <0.01

Table 2. Summary data for the 8 $\dot{V}O_2$ runs made on albacore no. 5 (11.5 kg). Data presentation is similar to Table 1 except that $\dot{V}O_2$ data are combined for the entire PO_2 range. Total duration of study, 9.2 h

Pre-run Interval (min)	50	17	32	36	26	17	11	13
Run no.	1	2	3	4	5	6	7	8
Duration (min)	62	17	26	41	99	22	35	48
°C	14.9	15.4	15.8	16.8	16.5	16.2	15.0	15.5
PO_2 range (torr)	312 – 112	160 – 107	200 – 114	181 – 62	400 – 52	184 – 75	150 – 60	240 – 140
Tailbeat[a] ($\bar{x}$) (Hz)	2.0	2.0	1.9	1.8	1.7	1.8	1.8	1.9
U[b] ($\bar{x}$) (L/s)	0.53	0.63	0.72	0.72	0.73	0.82	0.86	0.80
$\dot{V}O_2$ $\bar{x}$ (SE), ml/min	41 (2)	43 (9)	40 (5)	34 (4)	41 (3)	49 (5)	46 (4)	52 (3)

[a] All SE values <0.06
[b] All SE values <0.02

Table 3. Summary data for the 6 $\dot{V}O_2$ runs made for albacore no. 11 (8.5 kg). See text and Table 2 for details. Total duration of study, 6.7 h

Pre-run Interval (min)	21	21	16	19	16	55
Run no.	1	2	3	4	5	6
Duration (min)	20	19	45	64	53	50
°C	15.6	14.9	14.5	14.4	14.9	18.0
PO_2 range (torr)	195 – 111	172 – 108	214 – 78	305 – 104	335 – 124	380 – 59
Tailbeat[a] ($\bar{x}$) (Hz)	1.8	1.8	1.9	2.0	2.1	2.5
U[b] ($\bar{x}$) (L/s)	0.60	0.63	0.77	0.95	1.0	1.0
$\dot{V}O_2$ $\bar{x}$ (SE), ml/min	55 (6)	43 (4)	37 (2)	42 (2)	57 (4)	101 (9)

[a] SE <0.06
[b] SE <0.02

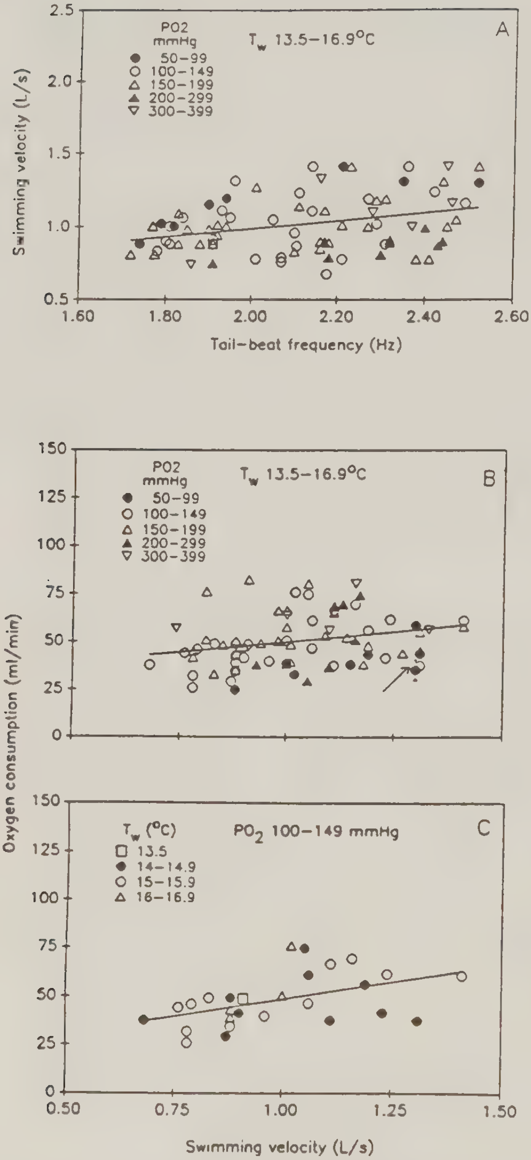


Fig. 1A. Effect of tail-beat frequency on the velocity of swimming albacore ($n = 9$) over a PO_2 range of 50–399 mmHg and water temperatures from 13.5° to 16.9°C. Equation for the significant ($P < 0.05$, t-test) regression line is $U = 0.43 + 0.28f$, where U = swimming velocity (L/s) and f = tail-beat frequency (Hz); $n = 81$. **B.** Effect of swimming velocity on the $\dot{V}O_2$ of albacore ($n = 9$). PO_2 and temperature ranges as in **A**. Equation for the significant regression is $\dot{V}O_2 = 28.5 + 21.5U$; $n = 77$. Value indicated by *arrow* is mean $\dot{V}O_2$ determined by Graham and Laurs (1982). **C.** $\dot{V}O_2$-swimming velocity data obtained for 9 albacore at 13.5°–16.9°C and within the PO_2 range of 100–149 mmHg. Equation for the significant regression is $\dot{V}O_2 = 5.9 + 43.3U$; $n = 28$

the $\dot{V}O_2$'s measured over the 50–99 mmHg range (dots, Fig. 1B) are consistently low compared to all other PO_2 ranges, suggesting a critical O_2 tension for albacore within this range (see below).

Figure 1C shows the $\dot{V}O_2$-velocity data obtained for albacore both at the range of temperatures (13.5°–16.9°C) and within a PO_2 range (100–149 mmHg) that they would naturally encounter. This reveals that at slow velocities, and in O_2 tensions typically experienced by this species, a doubling of the relative velocity (from 0.7 to 1.4 L/s) results in a near doubling of its $\dot{V}O_2$. This increment of $\dot{V}O_2$ increase is similar to that measured for other species at slow speeds (*Salmo gairdneri* [Webb 1971]; *Oncorhynchus nerka* [Brett and Glass 1973]; *Seriola quinqueradiata* [Tsukamoto and Chiba 1981]). The $\dot{V}O_2$ values measured for albacore at a range of speeds in this study also agree (Fig. 1C) with that determined at one speed and a temperature range of 15°–19°C by Graham and Laurs (1982), of 35.6 ml/min at 1.3 L/s. Finally, extrapolation of the velocity-$\dot{V}O_2$ data in Fig. 1C to "zero" L/s yields a "resting" $\dot{V}O_2$ of 12.8 ml/min. This is similar to the total standard (non-swimming) metabolic rates estimated for 10 kg individuals (at 25°C) of 3 tuna species, using regression equations provided by Brill (1987): yellowfin $\dot{V}O_2$ 12.5 ml/min, skipjack 17.6 ml/min, Kawakawa, 14.4 ml/min.

The findings demonstrate that albacore $\dot{V}O_2$ is affected by swimming speed and PO_2, as well as the time since fish capture. But our data do not show a significant mass effect, or an effect of temperature variations between 13.5° and 16.9°C (Fig. 1C) on the $\dot{V}O_2$ of this species. Thus, additional data are required. Yet, it is possible to analyse such multivariate data in order to identify other important determinants of albacore $\dot{V}O_2$. One procedure is to focus on the latter runs of each fish to lessen the "time since capture" variable. Figure 2A does this for fish no. 5, presenting only the $\dot{V}O_2$ data determined for runs 4–8. This again shows the slight effects of speed and water temperature on $\dot{V}O_2$, and the tendency for $\dot{V}O_2$ to decline at a PO_2 below 100 mmHg. Figure 2B contains data for runs 4, 5, and 6 of fish no. 11 and indicates good agreement for the $\dot{V}O_2$ of this fish during runs 4 and 5 (14.4° and 14.9°C) and that of fish no. 5. However, run 6, done at 18°C and with the fish swimming faster, shows a much higher $\dot{V}O_2$ that declines steadily with PO_2. Over the ambient range of 100–149 mmHg, the $\dot{V}O_2$ during run 6 is 1.8 times higher than the mean rate at cooler temperatures (83 vs 49 ml/min, Fig. 2B), and the Q_{10} for this difference is 4.5.

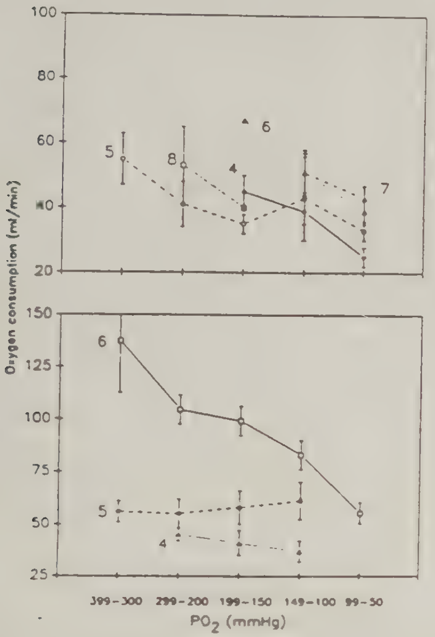


Fig. 2A. The $\dot{V}O_2$ ($\bar{x}$ ± SE) of albacore no. 5 as a function of PO_2 during runs *4*, *5*, *6*, *7*, and *8*. The mean water temperature and fish swimming velocity during each run are: run *4* (16.8°C, 0.72 L/s), run *5* (16.4°C, 0.76 L/s), run *6* (16.2°C, 0.82 L/s), run *7* (15.0°C, 0.87 L/s), and run *8* (15.5°C, 0.80 L/s). The hours after capture at which each run began are run *4* (4.7 h), run *5* (5.1 h), run *6* (7 h), run *7* (7.6 h), and run *8* (8.4 h). **B.** The $\dot{V}O_2$ ($\bar{x}$ ± SE) of albacore no. 11 as a function of PO_2 during runs *4*, *5*, and *6*. The mean water temperature and fish swimming velocity during each run are: run *4* (14.4°C, 0.77 L/s), run *5* (14.9°C, 0.86 L/s), run *6* (18.0°C, 1.0 L/s). Run *4* began 2.7 h post capture, run *5* 4.9 h post capture and run *6* at 5.8 h post capture. Note that the ordinal scales in A and B are different

Although it was obtained for only 1 fish, the finding that albacore metabolism increases dramatically at 18°C, supports previous results (Graham and Dickson 1981; Graham and Laurs 1982) showing that prolonged exposure to temperatures above 18°C adversely affects this species. Albacore usually swim in 9°–14°C water below the mixed layer (Laurs et al. 1977, 1980) but rush up into warm surface water to feed. Albacore swimming in 18°C water cannot shed metabolic heat and became increasingly hyperthermic (Graham and Dickson 1981), and whereas fish in the ocean can always exercise the behavioural option of returning to deeper, cooler water to shed excess heat, fish in the respirometer cannot do this.

The mean $\dot{V}O_2$ of fish no. 11 at 18°C and in hypoxia (50–99 mmHg), was reduced to about the same rate of fish no. 5 in cooler temperatures and in normoxia (Fig. 2), suggesting that increased temperature and hypoxia may have forced fish no. 11 to become partially anaerobic. Albacore may naturally experience PO_2's as low as 60% of air saturation (90 mmHg), but this usually happens in cooler (9°–12°C) water (Laurs and Lynn 1977; Cech et al. 1984). Although the thermally induced left-shift of the albacore O_2 dissociation curve should prove beneficial for O_2 uptake in warm hypoxic water, the large Q_{10} effect on its $\dot{V}O_2$ apparently outweighs this enhancement. Further studies that assess albacore responses to abrupt changes in temperature and O_2, such as those encountered by migration through and along oceanic fronts (Laurs and Lynn 1977), are needed, to define how factors such as swimming speed (i.e. heat production and $\dot{V}O_2$), haemoglobin-O_2 affinity, and behaviour may be integrated in metabolic responses to variable ambient conditions.

Acknowledgements. This work was supported by NSF DCB 84-16852 and DMB 85-00261. We thank the captain and the crew of the R.V. *David Starr Jordan* for assistance and support of this research.

References

Breisch EA, White FC, Jones MH, Laurs RM (1983) Ultrastructural morphometry of the myocardium of *Thunnus alalunga*. Cell Tissue Res 233: 427–438

Brett JR, Glass NR (1973) Metabolic rate and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to size and temperature. J Fish Res Board Can 30: 379–387

Brill RW (1987) On the standard metabolic rates of tropical tunas, including the effect of body size and acute temperature change. Fish Bull 85: 25–35

Cech JJ Jr, Laurs RM, Graham JB (1984) Temperature-induced changes in blood gas equilibria in the albacore, *Thunnus alalunga*, a warm-bodied tuna. J Exp Biol 199: 21–34

Graham JB, Dickson KA (1981) Physiological thermoregulation in the albacore *Thunnus alalunga*. Physiol Zool 54: 470–486

Graham JB, Laurs RM (1982) Metabolic rate of the albacore tuna *Thunnus alalunga*. Mar Biol 72: 1–6

Jones DR, Brill RW, Mense DC (1986) The influence of blood gas properties on gas tensions and pH of ventral and dorsal aortic blood in free-swimming tuna, *Euthynnus affinis*. J Exp Biol 120: 201–213

Lai NC, Graham JB, Lowell WR, Laurs RM (1987) Pericardial and vascular pressures and blood flow in the albacore tuna, *Thunnus alalunga*. Exp Biol. 46: 187–192

Laurs RM, Lynn RJ (1977) Seasonal migration of North Pacific albacore, *Thunnus alalunga*, into North American coastal waters: distribution, relative abundance, and association with Transition Zone waters. Fish Bull 75: 795–822

Laurs RM, Yuen HSH, Johnson JR (1977) Small-scale movements of albacore, *Thunnus alalunga*, in relation to ocean features as indicated by ultrasonic tracking and oceanographic sampling. Fish Bull 75: 347–355

Laurs RM, Ulevitch RJ, Morrison DC (1978) Estimates of blood volume in the albacore tuna. In: Sharp GD, Dizon AE (eds) The physiological ecology of tunas. Academic Press, New York, p 135

Laurs RM, Dotson RC, Dizon A, Jemison A (1980) Observations on swimming depth and ocean temperature telemetered from free-swimming albacore. In: Wild A (ed) Proc 31st Tuna Conf, Inter-American Tropical Tuna Commission, La Jolla, California, pp 33–34

Magnuson JJ (1978) Locomotion by scombrid fishes – hydrodynamics, morphology, and behavior. In: Hoar WS, Randall DJ (eds) Fish physiology, vol VII. Academic Press, New York, p 240

Perry SF, Daxboeck C, Emmett B, Hochachka PW, Brill RW (1985a) Effects of temperature change on acid-base regulation in skipjack tuna (*Katsuwonus pelamis*) blood. Comp Biochem Physiol 81A: 49–53

Perry SF, Daxboeck C, Emmett B, Hochachka PW, Brill RW (1985b) Effects of exhausting exercise on acid-base regulation in skipjack tuna (*Katsuwonus pelamis*) blood. Physiol Zool 58: 421–429

Prange HD (1976) Energetics of swimming of a sea turtle. J Exp Biol 64: 1–12

Tsukamoto K, Chiba K (1981) Oxygen consumption of yellowtail *Seriola quinqueradiata* in relation to swimming speed. Bull Jpn Soc Sci Fish 47: 673

Webb PW (1971) The swimming energetics of trout II. Oxygen consumption and swimming efficiency. J Exp Biol 55: 521–540

White FC, Kelly R, Kemper S, Schumacker PT, Gallagher KR, Laurs RM (1988) Organ blood flow haemodynamics and metabolism of the albacore tuna *Thunnus alalunga* (Bonnaterre). Exp Biol 47: 161–169

Received May 13, 1987/Accepted September 13, 1988

8922

Asian Fisheries Science 3(1989): 85-99.
Asian Fisheries Society, Manila, Philippines

Integration of United States, Thailand and Philippine Canned Tuna Markets

S.F. HERRICK, Jr. and D. SQUIRES

National Marine Fisheries Service
Southwest Fisheries Center
P.O. Box 271
La Jolla, California 92038, USA

Abstract

In this study we investigate price integration in the United States, Thailand and Philippine canned tuna markets by employing a dynamic model of spatial price differentials to determine how rapidly and completely price information is transmitted from one market to another over time. When the United States is assumed to be the central canned tuna market, we find that the Thai canned tuna market operates independently of price conditions in the United States. On the other hand, the Philippine market is well integrated with the United States market in the sense that a change in the United States price is quickly and effectively communicated to the Philippine market. These results are shown to have significant implications with regard to measures the United States might take to control the flow of canned tuna imports from Southeast Asia.

Introduction

In the early 1980s there began a rapid and substantial increase in the volume of canned tuna imported into the United States (US), the world's principal market for canned tuna. Intense competition from foreign processors began to develop when tuna packed in water started to surpass tuna canned in oil in popularity among US consumers, and rising production costs within the US tuna industry contributed to record high prices at the exvessel, wholesale and retail levels. This combination of events, plus a disparate tariff[1] on tuna

---

[1] The US tariff on imports of canned tuna packed in oil is different from that on imports of tuna not packed in oil. Tuna in oil is subject to a 35% tariff. Canned tuna not in oil is under a tariff rate quota which allows imports up to 20% of the previous year's domestic production, excluding production at American Samoa, to enter at 6% ad valorem, and imports above the quota level enter at 12.5% ad valorem.

canned in water, provided an unprecedented opportunity for low-cost imports to inundate the strongest growing segment of the US tuna market - tuna packed in water for sale to private label and institutional customers. From 1981 through 1986, the amount of canned tuna imported into the US more than tripled, increasing by more than 90% between 1983 and the end of 1986 alone. Thailand and the Philippines have become the major sources of these imports, together accounting for over 75% of the total imports in 1986 (Table 1).

Table 1. U.S. imports (tonnes) for consumption by principal sources of tuna in airtight containers (oil and water), 1983-1986.

Source	1983	1984	1985	1986
Canada	957	-	40	-
Ecuador	-	404	2,352	1,303
Indonesia	1,197	1,010	631	370
Japan	9,267	12,207	10,774	4,799
Malaysia	1,401	731	1,763	1,091
Philippines	14,554	10,102	13,999	12,719
South Korea	31	37	26	656
Spain[1]	60	97	153	108
Taiwan	8,504	8,152	10,669	12,990
Thailand	18,150	40,766	55,757	69,226
Other	1,482	271	1,085	952
Total	55,604	73,779	97,249	107,555

Notes: [1] Mainly oil packed.
Source: US Department of Commerce, Bureau of the Census.

Penetration of the US canned tuna market by Thai and Philippine processors was considered severe enough to prompt various members of the US industry (vessel owners, processors and cannery workers) to join together and petition the US International Trade Commission (ITC), under Section 201 of the Trade Act of 1974, for tariff relief from imports of canned tuna packed in water (Herrick and Koplin 1986). Although the industry was unsuccessful both in this attempt and in subsequent attempts to have protective tariff legislation enacted, industry's concern over the rapid growth of canned tuna imports indicates a need to assess the nature and extent of market integration between the Southeast Asian and US canned tuna markets, and thereby provide a fundamental understanding of how these markets work.

Markets may be integrated to different degrees and along some dimensions but not others. The flow of canned tuna from Southeast Asia into the US institutional/private label market is evidence of market integration on the basis of commodity flows. When the prices of a good that is produced in spatially separated markets are functionally related, market integration on the basis of price is said to exist. The purpose of this paper is to examine empirically price integration in the US, Thai and Philippine canned tuna markets. We restrict our attention to the institutional/private label canned tuna market in the US, since this market has been most greatly impacted by the rise in imports.

Market Integration and Price Analysis

Market Integration

Markets that are integrated on the basis of price are those in which prices do not behave independently. Geographical links or interregional trade has received the most attention. Two major issues of these spatial price linkages have been most frequently examined: whether markets are integrated, and if so, the extent and nature of this integration.

Dynamic Spatial Price Differentials

Ravallion (1986) recently proposed a dynamic model of spatial price differentials for a tradeable good which avoids the inferential dangers of static price correlations (Harriss 1979) and which also provides a more cohesive analytical procedure than other regression approaches (Timmer 1974; Harriss 1979; Petzel and Monke 1979-1980). By using *a priori* information on the most likely directions of price linkages from a central market to local markets, Ravallion's model permits each local price series (P_i) to have its own dynamic structure, allows for any correlated local seasonality or other characteristics, and provides for an interlinkage with other local markets. Moreover, the alternative hypotheses of market integration and market segmentation are encompassed within a more general model, thereby allowing for nested statistical testing. Finally, Ravallion's dynamic model distinguishes between the concepts of instantaneous market integration and the less restrictive idea of integration as a long-run target of the short-run dynamic adjustment process. Thus, if short-run adjustment is statistically rejected by the data, so that trade does not immediately adjust to spatial price differentials, it is possible to determine if there is any long-run tendency toward market integration.

Ravallion proposed the following econometric model of a T-period series of prices for N regions:

$$P_{it} = \sum_{j=1}^{J} a_{ij}P_{it-j} + \sum_{j=0}^{J} b_{ij}P_{1t-j} \qquad \ldots 1)$$

$$+ c_iX_{it} + e_{it}, \quad i = 2,\ldots,N,$$

where market 1 is the central market, X_i ($i = 1,2,\ldots,N$) is a matrix of nonprice influences on local markets, the e's are appropriate error processes, J is the number of time periods to be lagged, and the a's, b's and c's are parameters to be estimated.

Several hypotheses about interregional trade and market integration can be formulated as linear parameter restrictions on equation (1) (Ravallion):

1. *Market Segmentation.* The null hypothesis of local market segmentation states that changes in the central market prices will have no effect, immediate or lagged, on prices in the ith local market. Market i could be called segmented if:

$$b_{ij} = 0, \quad j = 0,1,\ldots,J, \qquad \ldots 2)$$

which can be determined by imposing the linear parameter restriction (2) on equation (1), and testing this restricted model against the unrestricted model of equation (1) with an F-test. Nonrejection of the restricted model or null hypothesis indicates that the price in local market i depends only on its own lagged values and local market characteristics.

2. *Short-Run Market Integration.* A price change in the central market will be immediately and fully passed on to the ith local market price if:

$$b_{i0} = 1 \qquad \ldots 3)$$

This hypothesis, in addition, requires that there be no lagged effects on prices in the future:

$$a_{ij} = b_{ij} = 0, \quad j = 1,2,\ldots,J \qquad \ldots 4)$$

If both (3) and (4) are accepted as parameter restrictions, then market i is integrated with the central market within one time period.

A weaker form of short-run market integration will also be tested, in which the lagged effects need only vanish on average:

$$\sum_{j=1}^{J} a_{ij} + \sum_{j=1}^{J} b_{ij} = 0 \qquad \ldots 5)$$

3. *Absence of Local Market Characteristics.* This hypothesis assumes that:

$$c_i = 0 \qquad \ldots 6)$$

where c_i is a vector if there is more than one local market characteristic. Testing this hypothesis is of interest when local prices are suspected to have different seasonality than the central market. In this case, X_{it} can be defined as a matrix of dummy variables.

4. *Long-Run Market Integration.* A long-run equilibrium is one in which market prices are constant over time, undisturbed by any local stochastic effects. Thus, when $P_{it} = P_i^*$, $i = 2,\ldots,N$, $P_{1t} = P_1^*$ and $e_{it} = 0$ for all t, equation (1) takes the form:

$$P_i^* = \frac{P_1^* \sum_{j=0}^{J} b_{ij} + X_{it}c_i}{1 - \sum_{j=1}^{J} a_{ij}} \qquad \ldots 7)$$

Long-run market integration now requires that:

$$\sum_{j=1}^{J} a_{ij} + \sum_{j=0}^{J} b_{ij} = 1 \qquad \ldots 8)$$

If this linear parameter restriction is not rejected by an F-test, then the short-run process of price adjustment described by the model is consistent with an equilibrium in which a unit increase in the central market price is fully passed on in local market prices.

Markets where previous central market prices and the past spatial price differentials are the primary determinants of local prices (rather than previous local prices) are well linked in the sense that supply and demand conditions in the central market are effectively communicated to local markets. The central market influences local market prices irrespective of previous local conditions in the long run, even though traders may fail to connect the two markets through commodity flows in the short run (Timmer 1974). Acceptance of the short-run restrictions [(3) and (4) or (5)] implies long-run market integration but the reverse is not necessarily true.

If the long-run market integration restriction is not rejected, then more efficient estimates of the remaining parameters and more powerful statistical tests are provided by reestimating the model with long-run market integration imposed. Equation (1) under long-run integration can be written in the following equivalent form (Ravallion 1986):

$$P_{it} - P_{it-1} = (a_{it} - 1)(P_{it-1} - P_{1t-1}) \qquad \ldots 9)$$

$$+ \sum_{j=2}^{J} a_{ij}(P_{it-j} - P_{1t-j}) + b_{10}(P_{1t} - P_{1t-1})$$

$$+ \sum_{j=1}^{J-1} (b_{10} - 1 + \sum_{k=1}^{J} a_{ik} + b_{ik})(P_{1t-j} - P_{1t-j-1})$$

$$+ c_i X_{it} + e_{it}.$$

Changes in local market prices, $P_{it} - P_{it-1}$, are then attributable to changes in central market prices and past spatial price differentials between local and central market prices. The latter variables allow for the possibility that the markets are not observed in an integrated equilibrium at a given time period, so that there is feedback from prior disequilibria.

Ravallion proposes the following sequence of nested F-tests for the different null hypotheses. First, test for long-run integration. If the null hypothesis of long-run market integration is rejected, then tests for short-run market integration and market segmentation are conducted. If long-run market integration is not rejected, then it should be imposed on the model with successive tests based on a restricted form such as equation (9).

It is possible that central and local market prices in equation (1) are formed simultaneously. Such an occurrence introduces a simultaneous equation problem, so that parameter estimates could be biased and inconsistent. Ravallion points out that the simultaneity in the system can be easily dealt with by using an appropriate instrumental variables estimator such as the two-stage least squares estimate of equation (1). This is obtained by replacing P_{1t} by its predicted values from the reduced form equation obtained from a regression of P_{1t} against its own lagged values, the lagged values of prices in all local markets, dummy variables, and time trend variables. The number of lagged periods might be limited by the corresponding degrees of freedom that are available.

Any lagged effects in the model are likely due to sluggishness in price adjustment, delays in transportation and expectations formation under price uncertainty (Ravallion). A lag of six months was chosen as a maximum period over which price responses would take place. In addition, two nonprice variables (X_{it}) were included as likely influences on local market prices. First, the influence of seasonality is accounted for by quarterly dummy variables for winter, spring, summer and fall. Second, the possibility of long-term effects from increasing Southeast Asian exports is described by a linear time trend.

The Data

Average monthly wholesale prices, 1983 through 1986, for a standard case of US water packed, private-label, light meat canned tuna were obtained from the National Marine Fisheries Service's Market News Service, Southwest Region. These are free-on-board (f.o.b.) prices at the canner's terminal. US prices were adjusted for inflation using the gross national product (GNP) implicit price deflator.

Prices for canned tuna processed in the Philippines and Thailand were obtained from the United Nations Food and Agriculture

Organization's Globefish Data Base for the years 1983 through 1986. The Globefish prices represent the monthly average cost and freight (c.f.) charges paid by US importers for a standard case of light meat, water packed canned tuna in US dollars. Thai and Philippine canned tuna prices were adjusted for inflation by the use of their respective GNP implicit price deflators.

Empirical Results

United States - Southeast Asian Market Integration

While the United States and Southeast Asian canned tuna markets are integrated by commodity flows, it is less clear if they are integrated by prices. The Ravallion approach allows a comprehensive assessment of this possible integration of these canned tuna markets by prices. Because of the large commodity flow of canned tuna from Southeast Asia to the United States, it is reasonable to assume that canned tuna price leadership, if any, is likely to come from the US. Consequently, the US wholesale market was specified as the central market and the Thai and Philippine markets were specified as the local markets. The unrestricted model given by equation (1) for six lagged periods ($J = 6$) was estimated by two-stage least squares. These regression results for the unrestricted model given in equation (1) are reported in Table 2. The autocorrelation and partial autocorrelation plots for the residuals for six lagged periods indicated that serial correlation did not present a problem of any importance.

The importance of the local market characteristics was first examined in each local market by an F-test of the null hypothesis given in equation (6) that the seasonal dummy variables and linear time trend are each zero. While the seasonal dummy variables and linear time trend did contribute in a significant way to the unrestricted model for price formation in the Philippine market, they were not important as a group in the formation of prices in the Thai market. Consequently, the final version of the unrestricted model given in equation (1) does not have any local market characteristics for Thailand, but the linear time trend and seasonal dummy variables are included for the Philippines. These final versions were then used for the hypotheses tests on the form of market integration.

Table 2. Parameter estimates of unrestricted dynamic model of spatial price differentials for United States, Thailand (Thai) and Philippine (Phil) canned tuna markets.

Variable	US=central Phil=local	US=central Thai=local	Thai=central Phil=local	Phil=central Thai=local
Intercept	-14.519	1.755	-3.295	3.253
	(10.69)	(0.091)	(1.295)	(1.846)
Spring dummy	-0.403	-0.308	-0.553	0.296
	(0.217)	(0.337)	(0.151)	(0.431)
Summer dummy	0.302	-0.072	-0.312	-0.042
	(0.275)	(0.306)	(0.183)	(0.270)
Fall dummy	0.083	-0.074	-0.167	-0.044
	(0.158)	(0.209)	(0.124)	(0.184)
Trend	0.084	0.010	-0.036	0.021
	(0.061)	(0.115)	(0.010)	(0.019)
Prices				
Local [t-1]	0.494	0.694	0.111	0.638
	(0.178)	(0.252)	(0.168)	(0.214)
Local [t-2]	0.180	-0.051	0.022	-0.087
	(0.188)	(0.245)	(0.173)	(0.231)
Local [t-3]	0.278	0.148	0.123	-0.122
	(0.211)	(0.436)	(0.191)	(0.255)
Local [t-4]	0.102	-0.304	0.402	-0.399
	(0.188)	(0.240)	(0.149)	(0.223)
Local [t-5]	-0.155	0.117	-0.050	0.251
	(0.195)	(0.267)	(0.150)	(0.252)
Local [t-6]	-0.111	0.132	-0.104	0.085
	(0.189)	(0.201)	(0.141)	(0.244)
Central [t-0]	1.341	-0.001	0.417	1.004
	(0.675)	(1.586)	(0.346)	(0.627)
Central [t-1]	-0.679	0.040	-0.089	-0.450
	(0.458)	(0.800)	(0.282)	(0.283)
Central [t-2]	0.018	0.037	0.039	0.068
	(0.302)	(0.358)	(0.175)	(0.226)
Central [t-3]	0.682	0.354	0.064	-0.127
	(0.330)	(0.471)	(0.164)	(0.249)
Central [t-4]	-0.219	-0.314	0.198	-0.192
	(0.312)	(0.361)	(0.174)	(0.192)
Central [t-5]	0.075	0.072	0.147	0.024
	(0.310)	(0.368)	(0.195)	(0.194)
Central [t-6]	-0.138	-0.162	0.154	0.057
	(0.330)	(0.424)	(0.180)	(0.185)

Note: Two-stage least squares estimates of unrestricted model given by equation (1). [t-j] denotes current time t less j time periods. Standard deviations in parentheses.

The results from these F-tests are reported in Table 3, and all hypothesis tests were evaluated at a 1% level of significance.

Table 3. Hypothesis tests for the integration of United States, Thailand (Thai), and Philippine (Phil) canned tuna markets.

	Null hypothesis	Central market/Local market US/Thai	 US/Phil[1]	 Thai/Phil[1]	 Phil/Thai
1.	No local market characteristics (time trend, seasonality)	.537* (4,24)	3.193 (4,24)	6.719 (4,24)	.765* (4,24)
2.	Long-run integration	8.203 (1,28)	1.480* (1,24)	.389* (1,24)	5.322 (1,28)
3.	Short-run integration	37.860 (12,28)	1.824* (12,25)	4.692 (12,25)	17.848 (13,28)
4.	Short-run integration (weak form)	24.255 (2,28)		5.523 (2,25)	5.407 (2,28)
5.	Market segmentation	1.121* (7,28)			1.492* (7,28)

Notes: The unrestricted model is equation (1) for J=6 estimated using two stages least squares. The table gives F-tests of the linear restrictions on the model implied by each null hypothesis. Distributions of F-test statistics given in parentheses of form (numerator degrees of freedom, denominator degrees of freedom).

[1] Short-run integration tests conditional upon maintained hypothesis of long-run integration as given in equation (9).

*Indicates non-rejection of null hypothesis at 1% level of significance.

The null hypothesis of long-run market integration between the US central market and the Thailand local market, following equation (8), was rejected. Tests for the short-run market integration between the US central market and the Thai local market were then performed with both the strong, equations (3) and (4), and weak, equation (5), forms of short-run market integration being rejected. Based on these findings we tested the alternative null hypothesis that the local Thai market was segmented from the US central market, equation (2), and it was decisively not rejected. The overall results, reported in Table 3, indicate that market segmentation by prices is the most likely relationship between the Thai local and US central canned tuna markets.

The null hypothesis of long-run market integration by prices between the US central market and the Philippine local market was not rejected. Therefore, in order to obtain more efficient estimates of the parameters and more powerful statistical tests for the short-run market integration hypotheses tests for the Philippines, the model was respecified with long-run integration imposed as in equation (9). All tests were then conducted against this restricted form, and it was found that the null hypothesis of strong short-run market integration between the US central market and the Philippines local market could not be rejected. (Regression results are available from the authors upon request.)

To summarize the empirical results to this point, the US central and Thailand local wholesale, canned tuna markets were likely to have been price segmented over the period 1983-1986. Under these conditions, changes in US market prices will have no effect, immediate or lagged, on the Thailand local market. Instead, the Thai market price depends only upon its own lagged values: Thai canned tuna markets operated independently of the US market. Should the issue of tariff relief from canned tuna imports resurface, then the general lack of Thai responsiveness to US price changes and other market information could be a major consideration in policy formation.

During the 1983-1986 period, the US central and Philippine local wholesale, canned tuna markets were well integrated by prices in the sense of a long-run tendency in the short-run adjustment process. Continuation of these circumstances indicates that changes in Philippine prices can be attributed to changes in US prices and past spatial price differentials between the US and Philippine markets. Supply and demand conditions in the US central market will be communicated effectively to the Philippine local market and influence prices there irrespective of previous local conditions.

Southeast Asian Market Integration

Because the US did not emerge as the overall price leader with respect to canned tuna price formation in Thailand and the Philippines, we extended our investigation to examine price formation solely within these two Southeast Asian markets.

The unrestricted model, equation (1), was first estimated with the Philippine market as the local market and the Thai market as the central market for six lagged periods (J = 6). The regression results are shown in Table 2. Local market characteristics were found to significantly influence price formation in the Philippine market. The null hypothesis of long-run integration between the Thai central market and the Philippine local market was not rejected and the model was reestimated, equation (9), with long-run integration imposed to further test for short-run market integration. (Regression results are available from the authors upon request.) The null hypotheses of strong and weak short-run market integration between the Thai central market and the Philippine local market were each rejected. The results from these hypotheses tests are shown in Table 3.

Secondly, the Thai market was specified as the local market and the Philippines as the central market. The unrestricted, six-period lag (J = 6) model, equation (1), was first estimated. The regression results are reported in Table 2. Based on an F-test, local market characteristics did not make a statistically significant contribution to this model's overall explanatory power, and a revised version, without these variables, was estimated for the hypotheses tests on the form of market integration.

After the null hypothesis for long-run market integration between the Philippine central market and the Thai local market was rejected, tests for short-run market integration were conducted. Null hypotheses for both the strong and weak forms of short-run market integration were rejected. Given these findings, we tested the alternative null hypothesis of market segmentation for Thailand (as the local market) which indicated conclusively that Thai prices, during the period of interest, were formed independently of Philippine prices. Table 3 presents the results of these hypotheses tests.

In summary, Philippine canned tuna prices did not appear to exert any influence, immediate or lagged, on the current price in the Thai market during the 1983-1986 period. As in the case where the US was hypothesized to be the central market, the price in the Thai market depends only upon its own lagged values. On the other hand, the current price in the Philippine market did depend on current and past prices in the Thai market based on our finding of long-run market integration when the Philippines was specified as the local market and Thailand was the central market.

Conclusions

In this study, we examined the US, Thailand and Philippine canned tuna markets for several forms of long-run and short-run integration by prices.

We found that the Thai canned tuna market operated independently of the price conditions in the US and Philippine markets, i.e., market segmentation occurred. Thus, changes in the US and Philippine market prices during the 1983-1986 period had no effect, immediate or lagged, on the Thai market. The Thai market price instead depended only upon its own lagged values.

The Philippine market during this period was responsive to supply and demand conditions in both the US and Thai markets. The Philippines and US markets were well integrated in the sense that a change in the US price was quickly and effectively communicated to the Philippine market within one month, and exerted significant influence on the Philippine market prices.

The Philippine and Thai markets were integrated by market prices in the long run, but not in the short run. Although the latest price change in the Thai market was not immediately and fully passed on to the Philippine market, Thai prices over the previous six months did have a significant effect on the current price in the Philippine market. To the extent that Philippine prices respond to Thai prices, but not vice versa, this establishes Thailand as a price leader.

Our findings concerning Thai market integration on the basis of price, in conjunction with the relative volumes of US imports of canned tuna from Thailand - market integration on the basis of commodity flows - during the period 1983-1986, are not uniquely associated with a particular type of market organization, or industry structure.[2]

The empirical results can be interpreted in several different ways. First, the results are consistent with the situation within the Thai tuna processing industry recently described by Crough (1987) where excess canning capacity exists in a number of competing firms utilizing some of the most advanced canning technology available.

---

[2] The analysis covers a period of rapid expansion of tuna markets in the Southeast Asian region, 1983 through 1986. Therefore, the results may not be indicative of the long-term industry organization that may evolve within the region, and hence, long-term relationships with export markets such as the US.

Such circumstances would provide an opportunity, and an incentive, for firms to expand production since increased output would be realized at constant or even decreasing unit costs. Thus, it would not be unexpected to observe increased exports of Thai canned tuna while prices remain relatively unresponsive to changing supply and demand conditions in the US market.

Results from our analysis of price formation in the Thai canned tuna market are also in keeping with a monopsonistic or an oligopsonistic intermediate market for Thai canned tuna destined for the US wholesale market. With either a single US importer/purchaser of the Thai product, or with collusion among only a few significant purchasers, we would expect greater disparity between the price paid to Thai processors - the import price which we observe - and wholesale price observed for the comparable US product. By virtue of their concentrated purchasing power, importers are in a position to establish an import price that is relatively insensitive to changing supply and demand conditions in the US wholesale canned tuna market.

Finally, our results could be taken as evidence of a trade policy on the part of Thailand aimed at securing a dominant share of the private label/institutional market for canned tuna in the United States. Such a policy would not only erect barriers for potential entrants into the US market, but as in the case of the Philippines, creates a price leadership situation in which existing competitors must constantly respond to Thai prices in order to maintain a share of the market.

Further research is required to determine the appropriateness of the Southeast Asian-US canned tuna market scenarios presented above, and possibly other alternatives. Nonetheless, any interest of the United States in guiding the flow of canned tuna imports might best be dealt with through import quotas rather than increased tariffs. The former would directly limit the volume of imports, while the latter might not. The impact of an increased tariff is less certain, since Thai exports have not been responsive to changes in US supply and demand conditions. If Thailand is willing to accept lower prices in order to maintain or increase canned tuna exports in response to an increased tariff, the benefits from an increased tariff in the form of increased public revenues may be more than offset by the costs to the US tuna industry from further erosion of its market share.

Acknowledgements

The authors wish to thank Dan Huppert, Izadore Barrett and an anonymous reviewer for their comments and suggestions. Nonetheless, the authors remain responsible for any remaining errors. The results and conclusions are not necessarily those of the National Marine Fisheries Service.

References

Crough, G.J. 1987. The development of the tuna industry in Thailand, p. 187-200. *In* D.J. Doulman (ed.) The development of the tuna industry in the Pacific Islands Region: an analysis of options. East-West Center, Honolulu.

Harriss, B. 1979. There is method in my madness: Or is it vice versa? Measuring agricultural market performance. Food Res. Inst. Stud. 17: 197-218.

Herrick, Jr., S.F. and S.J. Koplin. 1986. U.S. tuna trade summary, 1984. Mar. Fish. Rev. 48: 28-37.

Petzel, T.E. and E.A. Monke. 1979-80. The integration of the international rice market. Food Res. Inst. Stud. 27: 307-326.

Ravallion, M. 1986. Testing market integration. Am. J. Agric. Econ. 68: 102-109.

Timmer, C.P. 1974. A model of rice marketing margins in Indonesia. Food Res. Inst. Stud. 13: 145-167.

Manuscript received 30 September 1988; accepted 14 July 1989

8923

American Fisheries Society Symposium 6:83–91, 1989

Optimal Harvesting Policies for the Widow Rockfish Fishery

JOSEPH E. HIGHTOWER AND WILLIAM H. LENARZ

National Marine Fisheries Service, Southwest Fisheries Center Tiburon Laboratory
3150 Paradise Drive, Tiburon, California 94920, USA

Abstract.—We developed optimal harvesting policies for the widow rockfish *Sebastes entomelas* fishery using a microcomputer-based age-structured model. We compared traditional constant effort policies to more complex escapement policies (control of spawning stock size) using three criteria: the difficulty of estimating policy parameters, the average harvest obtained, and the variability in harvest. Substantial computational effort was required to obtain optimal estimates for the two-parameter escapement policies, and a single run usually required 24 h or more to complete on a microcomputer. Conservative escapement policies were similar in form and in performance to constant effort policies. Mean harvest under the least-conservative escapement policy was only about 2% greater than mean harvest under a constant effort policy, yet variability in harvest increased by 49%. For stocks where density dependence is not strong, we suggest that only minor improvement will be gained through the use of two-parameter escapement policies.

Harvest guidelines for multiaged fish stocks traditionally have been based on either constant catch or constant effort policies. Both of these policies can be viewed as special cases of a more general harvesting policy proposed by Ruppert et al. (1984):

$$h = \begin{cases} \gamma(S - \delta)^{\theta} & \text{if } S > \delta \\ 0 & \text{otherwise;} \end{cases} \qquad (1)$$

h is harvest, S is stock size, and γ, δ, and θ are policy parameters. The parameter δ represents the minimum acceptable stock size; the fishery would be closed whenever $S \leq \delta$. An advantage of this more general harvesting policy is that an optimization routine can be used to determine which type of policy is most appropriate for a particular fishery and management objective. Special cases of interest are policies that provide constant catch ($\theta = 0$) or approximately constant effort ($\delta = 0$, $\theta = 1$) or escapement ($\theta = 1$, $\delta > 0$, γ properly chosen) (Ruppert et al. 1985).

Although it is possible to estimate the optimal values of all three parameters, more might be learned about policy behavior by fixing θ at several different levels (Ruppert et al. 1984). An advantage of setting $\theta = 1.0$ is that harvest will then be a linear function of stock size. A disadvantage is that annual fluctuations in harvest will tend to be large, and for that reason, $\theta = 0.5$ has also been used as a more conservative alternative (Ruppert et al. 1984, 1985).

The objective of this study was to develop optimal harvesting policies for the widow rockfish *Sebastes entomelas* fishery. These policies were obtained by using a microcomputer-based age-structured model. We compared traditional constant effort policies with escapement policies obtained by using equation (1). Policy performance was evaluated on the basis of average harvest obtained, variability in harvest, and the difficulty in obtaining parameter estimates.

History of the Fishery

Landings of widow rockfish were small prior to 1979 because processors believed that this fish had several negative characteristics, including a short shelf life for both fresh and frozen products and poor quality of the defrosted product (Ueber 1987). Advances in fishing and processing techniques around 1978 resulted in improved marketability. Widow rockfish fillets began to be sold in volume, and there were few complaints about quality (Ueber 1987). Landings increased rapidly to a peak of 27,691 tonnes in 1981, then declined to about 10,000 tonnes in 1983–1985 (Table 1). The rapid decline in harvest can be attributed not only to the reduction in stock size due to fishing, but also to restrictions on harvest implemented by the Pacific Fishery Management Council (PFMC). The annual quota, referred to as optimum yield (OY), was based on an estimate of acceptable biological catch (ABC) but sometimes exceeded ABC due to nonbiological considerations (Table 1). The ABC is determined annually and may be lower or higher than maximum sustained yield, depending on the current condition of the stock (PFMC 1982).

Assessment during this early phase of the fishery was difficult not only because historical catch data were not available, but also because tradi-

TABLE 1.—Total weight landed (Lenarz and Hightower in PFMC 1985), optimal yield (OY), and acceptable biological catch (ABC), in tonnes, for widow rockfish in the Washington–Oregon–California fishery, 1979–1986 (PFMC 1985).

Year	Total landings	OY	ABC
1979	4,941		
1980	20,390		
1981	27,691		
1982	26,513	26,000	16,800[a]
1983	10,211	10,500	10,500
1984	9,722	9,300	9,300
1985	9,023[b]	9,300	7,400
1986		10,200[b]	9,300

[a] Gunderson (1984).

[b] Preliminary reports from the Pacific Fishery Information Network (PacFIN).

tional bottom-trawl surveys provided little information about this pelagic stock (PFMC 1982). In one respect, however, management is simpler than for most species in the Pacific coast groundfish fishery. The midwater fishery for widow rockfish is highly directed, with minimal bycatch, so restrictions on harvest do not directly affect catches of other species.

Methods

Estimating Model Parameters

Lenarz and Hightower[1] used cohort analysis (Murphy 1965) of the 1980–1984 catch-at-age data to estimate age-specific fishing mortality (F) for widow rockfish. A separate analysis was done for natural mortalities (M) of 0.15 and 0.20 (assumed to be lower and upper bounds for M). For this study, we scaled 1980–1984 average age-specific fishing mortalities so that relative vulnerability ranged from 0 to 1 (Table 2). Using those values as catchability coefficients, fishing effort corresponded to the F at ages 9 and 10, the estimated ages at which fishing mortality is greatest (and assumed to be equal). Length at age was obtained as an average of values from sex-specific von Bertalanffy growth curves (Lenarz 1987). Weight at age was then obtained from a pooled length–weight relationship (Barss and Echeverria 1987; Table 2). We obtained an index of fecundity (Table 2) by multiplying weight at age and percent maturity (Barss and Echeverria 1987).

Lenarz and Hightower[1] used a deterministic model to represent the spawner–recruit relationship, and they assumed that the number of age-4 recruits (x_4) and the size of spawning stock were either independent or weakly dependent. For this study, we considered only the latter, more conservative assumption because the optimal harvest-maximizing policy may not exist if recruitment is assumed to be constant. We used a stochastic version of the model and obtained an estimate of variability in recruitment by fitting the model

$$x_4 = \mu \exp(v);$$

μ represents mean recruitment, and v represents a normally distributed random variate with mean 0 and variance σ^2. An estimate of σ^2 was obtained

TABLE 2.—Parameter estimates for an age-structured model of the widow rockfish fishery. Number-at-age vectors at the beginning of 1986 were obtained from results of cohort analysis for assumed natural mortalities (M) of 0.15 or 0.20. Parameter estimates for the Beverton–Holt spawner–recruit relationship were $\alpha = 0.0472$, $\beta = 0.8560$, and lognormal error variance $\sigma^2 = 0.8665$ for $M = 0.15$; $\alpha = 0.0365$, $\beta = 0.6336$, and $\sigma^2 = 1.0438$ for $M = 0.20$.

Age years	Fecundity index[a]	Weight (kg)	Catchability[b]		Number at age (millions)	
			$M = 0.15$	$M = 0.20$	$M = 0.15$	$M = 0.20$
4	0.000	0.4	0.038	0.036	21.7	30.9
5	0.075	0.5	0.179	0.176	18.4	25.1
6	0.102	0.6	0.499	0.494	2.4	2.2
7	0.490	0.7	0.716	0.715	8.3	7.9
8	0.711	0.9	0.886	0.887	16.6	15.6
9	0.950	1.0	1.000	1.000	8.9	8.3
10	1.067	1.1	1.000	1.000	1.2	1.1
11	1.164	1.2	0.826	0.835	0.9	0.8
12	1.300	1.3	0.601	0.614	0.4	0.4
13+	1.600	1.6	0.601	0.614	9.6	8.7

[a] Fecundity index = weight × proportion mature.

[b] Catchability = vulnerability to fishing (1.0 = fully recruited).

---

[1] Lenarz, W. H., and J. E. Hightower. 1985. Status of the widow rockfish fishery. This document is included in an annual report published by the Pacific Fishery Management Council (PFMC 1985). It contains a detailed description of assessment methods as well as landings data, catch-at-age data, and age-specific estimates of fishing mortality and population size obtained from cohort analysis.

as the variance of $\log_e(x_4)$. We then obtained estimates of the parameters α and β for a Beverton–Holt spawner–recruit curve of the form,

$$x_4 = 1/(\alpha + \beta/S),$$

by assuming that (1) the spawning stock in 1980 was representative of the spawning stock prior to exploitation (S_∞); (2) μ was an estimate of recruitment at S_∞; and (3) recruitment would be reduced by 10% if spawning stock was reduced by 50% from S_∞. This approach was used because we did not have sufficient data on spawning stock size and recruitment to estimate α and β directly. Because few studies have shown a statistically significant relationship between spawning stock size and recruitment (Hennemuth 1979), we viewed the above approach as a conservative way of estimating the productivity of the fishery.

Model of the Fishery

The number-at-age vector in year $k + 1$ ($x[k+1]$) was obtained from $x[k]$ by using the following equations:

$$x_{i+1}[k+1] = x_i[k] \exp(-M - q_i f[k]);$$
$$k = 0, \ldots, N - 1;$$
$$i = 4, \ldots, \lambda - 2;$$

$$x_\lambda[k+1] = x_{\lambda-1}[k] \exp(-M - q_{\lambda-1} f[k]) + x_\lambda[k] \exp(-M - q_\lambda f[k]);$$

$x_i[k]$ = number of age-i fish in year k;
λ = maximum age-class used in the model;
q_i = catchability coefficient for age-i fish;
M = annual instantaneous natural mortality (assumed to be constant over all ages);
$f[k]$ = level of fishing effort in year k.

Fishing effort was permitted to vary from 0 to $f_{\max}$; $f_{\max}$ was assumed to be 1.0 for widow rockfish. Harvest in year k was defined as

$$h[k] = \sum_{i=4}^{\lambda} x_i[k]\, w_i\, q_i\, f[k] \cdot \{1 - \exp(-M - q_i f[k])\}/(M + q_i f[k]);$$

w_i was the average weight of age-i fish.

Optimization Methodology

We identified the constant effort policies that maximized harvest by simulating the fishery at effort levels ranging from 0.0 to 1.0. Each simulation was 65 years in length, or five times λ, the maximum age-class used in the model. Using a replication–deletion approach (Law and Kelton 1982), we estimated mean harvest from the last 33 harvests of each 65-year period for each of 100 replicates. This approach was used to minimize the influence of the starting conditions.

A 65-year horizon also was used to obtain parameter estimates for the escapement policies. We did a limited number of optimization runs using shorter and longer planning horizons but found that the optimal policy for a 25-year horizon was to deplete the stock. Results for a 100-year horizon were similar to those reported here.

Following Ruppert et al. (1984, 1985), we defined an optimal escapement policy (control of spawning potential) as one that maximized harvest, $\Sigma h[k]$, or log-harvest, $\Sigma \log_e(h[k] + 1)$; harvest was determined from equation (1) and spawning stock size was used as a measure of spawning potential. These management objectives were selected to represent extremes along a risk continuum, representing willingness to accept risk (and fluctuations in harvest) for $\Sigma h[k]$ and extreme risk aversion for $\Sigma \log_e(h[k] + 1)$ (Ruppert et al. 1985).

Because the escapement rule determines only total harvest, the fishing mortality that produce that harvest must be determined iteratively. We used Newton's method (Dew and James 1983) to determine fishing effort as

$$f_{j+1} = f_j - (h_j - h[k])/h'[k];$$

f_j is the level of fishing effort at step j in the iterative sequence, h_j is the jth estimate of $h[k]$, and $h'[k]$ is the derivative of $h[k]$ obtained at $f = f_j$. We obtained acceptably accurate estimates more quickly using Newton's method than using a binary search but, nevertheless, simulation runs with an escapement rule took substantially longer than runs with constant effort.

We used an iterative approach termed stochastic approximation to estimate optimal values of γ and δ (Ruppert et al. 1984, 1985). The approach we used was essentially equivalent to the approach Ruppert et al. (1984) used, except our version was intended for use with several species so it was slightly less specific. Default starting values for γ and δ were obtained by using a deterministic version of the model to (1) solve iteratively for the level of fishing effort producing maximum sustained yield (f_{msy}), (2) determine h_{msy} and S_{msy}, and (3) obtain $\gamma = h_{\text{msy}}/S^{\theta}_{\text{msy}}$ for $\delta = 0$. To account for the effect of a lognormal error term, expected recruitment was estimated as

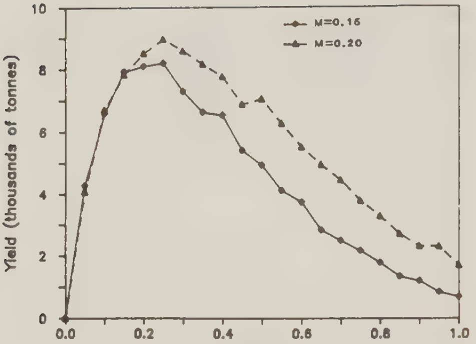


FIGURE 1.—Relationship between yield and fishing effort (fishing mortality for fully recruited fish) for widow rockfish at two levels of natural mortality (*M*).

$$1/(\alpha + \beta/S)\ \exp(\sigma^2/2).$$

This modification was used because $\exp(\sigma^2/2)$ was the expected value of the lognormal random variate $\exp(v)$; v was normally distributed with mean 0 and variance σ^2 (Hogg and Craig 1978). The assumption that $\delta = 0$ was used to begin the search in the region where closures would be infrequent. In addition, setting δ to 0 insured that the starting policy would perform similarly to a constant effort policy, a type that has performed well in earlier optimization studies (Swartzman et al. 1983; Getz 1985). This starting point worked reasonably well in the cases we examined even though final δ values were not necessarily close to 0. It was important to obtain good starting estimates of γ and δ; otherwise, the estimate of the Hessian (matrix of second derivatives) was poor, and estimates of γ and δ converged slowly or not at all. Because the optimum for the deterministic model differed from that for the stochastic model, we refined the starting estimates of γ and δ using a steepest ascent approach (Kiefer and Wolfowitz 1952) before attempting to estimate the Hessian. (The optimization and simulation routines used in this study are incorporated into the microcomputer program GENMOD. Copies of this program can be obtained from the American Fisheries Society Computer Users Section library.)

Results and Discussion

Steady-state yield under the constant effort policies appeared to be highest when effort (F_9) was about 0.25 (Figure 1), and that value was used in the comparative studies that follow. The relationship between yield and effort was similar for both values of natural mortality. In previous studies with a deterministic model, Lenarz and Hightower[1] suggested that F_9 should be about 0.30. Results were slightly more conservative in this study because the constant recruitment case was not considered.

Optimal parameter estimates for the escapement policies were difficult to obtain on a microcomputer, often requiring several hundred iterations that took 24 h or more to complete. The run length can be attributed, in part, to the stringency of the stopping rule (Ruppert et al. 1984) and to the use of an iterative routine to obtain fishing mortality. However, the primary reason was that nine 65-year simulation runs were made at each iteration to numerically estimate the first and second derivatives of harvest with respect to γ and δ. These derivatives were used in the stochastic approximation routine to obtain updated estimates of the parameters (Ruppert et al. 1984). Our observations regarding the number of iterations required were similar to those of Ruppert et al. (1984), although the implications were greater in our study because we were using microcomputers.

For the harvest-maximizing policies, we obtained similar values for δ with $\theta = 0.5$ and $\theta = 1.0$ (Table 3; Figure 2). To better understand the implications of different δ values, we estimated steady-state spawning stock at constant levels of fishing effort ranging from 0.0 to 1.0 (Figure 3). Results for both levels of natural mortality suggested that spawning stock could drop below 25,000 tonnes periodically, because average spawning stock was only about 40,000 tonnes when fishing at the MSY level ($F_9 = 0.25$). Thus, under any of the four harvest-maximizing policies, occasional closures would be expected. Using additional simulation studies, we estimated that the fishery would be closed from 0.8 to 14.8% of the time if a harvest-maximizing policy was used (Figure 4).

Our results for the log-harvest policies when $\theta = 1.0$ were similar to those obtained by Ruppert et al. (1985) in that δ was less than 0, so no closure could occur under that policy (Table 3; Figure 2). Closures would be unexpected for $\theta = 0.5$ because a spawning stock of about 10,000 tonnes would correspond to a fishing mortality rate of twice the optimal level (Figure 3). These results are in agreement with those of earlier studies in that policies for maximizing log harvest limit

TABLE 3.—Parameter estimates for the optimal harvesting policies, estimate of steady-state mean harvest, coefficients of variation (CV = 100 × SD/mean) for harvest in the final year of the planning horizon (year 65, or 2051), and recommended harvests for widow rockfish in 1986 for assumed natural mortalities (*M*) of 0.15 or 0.20. Parameters θ and γ are dimensionless; δ, mean harvest, and recommended 1986 harvest are given in thousands of tonnes.

Policy	θ	γ	δ	Mean harvest	CV in year 65	Recom-mended 1986 harvest
			M = 0.15			
Constant effort				7.79	39	8.62
$\log_e$(harvest)	0.5	1.569	12.893	7.73	35	8.78
$\log_e$(harvest)	1.0	0.181	−3.508	7.79	38	8.63
Harvest	0.5	2.581	27.373	7.97	49	10.57
Harvest	1.0	0.643	25.018	7.96	58	12.31
			M = 0.20			
Constant effort				8.63	48	8.04
$\log_e$(harvest)	0.5	1.727	11.075	8.40	40	9.53
$\log_e$(harvest)	1.0	0.218	−3.203	8.52	49	9.75
Harvest	0.5	3.658	26.960	8.82	69	13.95
Harvest	1.0	0.674	20.707	8.80	68	14.01

variability in harvest and reduce the frequency of closure (Mendelssohn 1982; Deriso 1985; Ruppert et al. 1985).

The short-term management implications of the five optimal policies were examined by determining the recommended 1986 harvest under each policy. Results from the escapement policies for maximizing log harvest (Table 3) were in good agreement with the earlier recommendation that the acceptable biological catch be set at 9,300 tonnes (Table 1). Results for the harvest-maximizing policies suggested that the 1986 harvest could be somewhat higher; however, the penalty for increased harvest would be increased variability in harvest (Table 3). Fishermen have often stressed the importance of continuity in harvest regulations; thus, we believe that more weight should be given to the more conservative policies for maximizing log harvest.

We evaluated the long-term performance of the escapement policies by comparing the results with

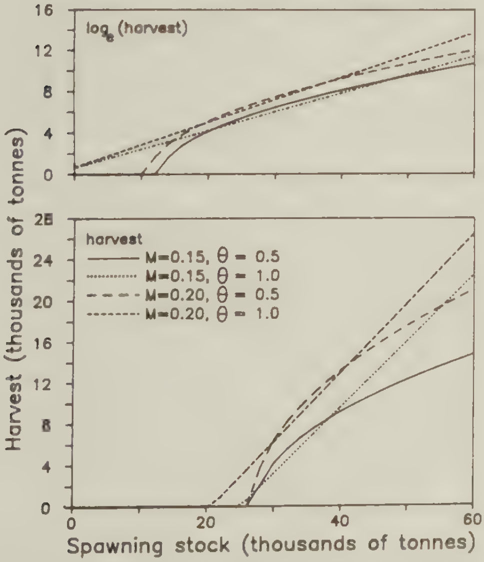


FIGURE 2.—Escapement policies for maximizing $\log_e$ (harvest) and harvest obtained for widow rockfish at two levels of natural mortality (*M*) and two values for the policy parameter θ.

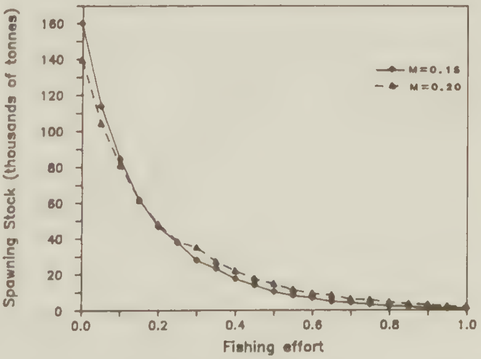


FIGURE 3.—Relationship between mean spawning stock and fishing effort (fishing mortality for fully recruited fish) for widow rockfish at two levels of natural mortality (*M*).

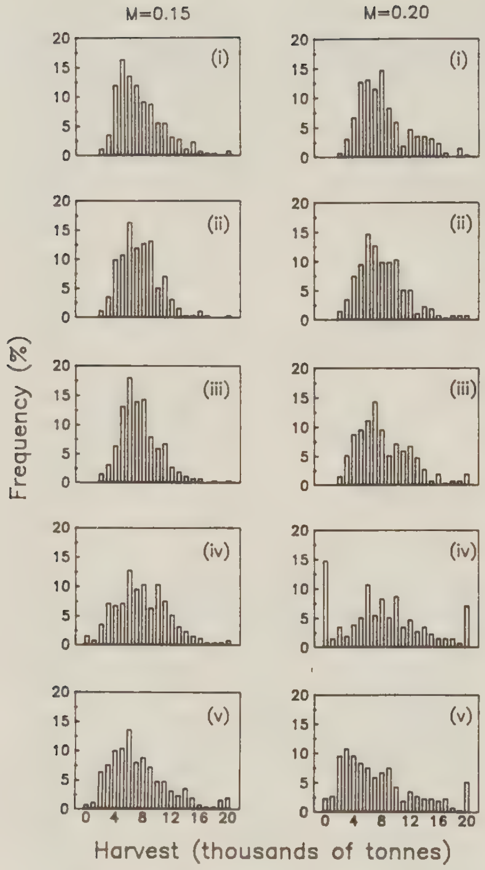


FIGURE 4.—Frequency distributions for annual harvests of widow rockfish obtained at two levels of natural mortality (*M*) with the use of (**i**) constant effort policies, (**ii**) policies for maximizing $\log_e$(harvest) with policy parameter $\theta = 0.5$ and (**iii**) $\theta = 1.0$, and (**iv**) policies for maximizing harvest with $\theta = 0.5$ and (**v**) $\theta = 1.0$. Each sample distribution is based on 250 independent observations of harvest in year 65.

those of constant effort policies. In each case, mean harvest was estimated from 250 replicate 65-year simulations by the replication–deletion approach described earlier (Table 3). We also calculated the coefficients of variation for harvest in year 65 as a measure of year-to-year variability in harvest. A common random-number stream was used at each level of natural mortality so that differences in mean harvest could be attributed directly to differences in policy performance. Our results indicate that, for widow rockfish, mean harvest under the least conservative escapement policy was only about 2% greater than mean harvest under a constant effort policy. This small increase in harvest was accompanied by a 49% increase in the variability of harvest. Under the most conservative escapement policy, both mean harvest and variability in harvest were slightly lower than under the constant effort policy. For the log-escapement policies with $\theta = 1.0$, results were quite similar to those from constant effort policies. Similar performance would be expected because the policies for maximizing log harvest were similar in form to constant effort policies (Figure 2), and because constant effort policies maximize log harvest for some models (Deriso 1985).

Much better relative performance for the escapement policies was reported by Ruppert et al. (1985), who examined the same five policies for the Atlantic menhaden *Brevoortia tyrannus* fishery. They reported that steady-state yield was nearly 20% higher under the four escapement policies than under the optimal constant effort policy. Variability in yield was comparable for the constant effort policy and three of the four escapement policies, with a considerably higher variance for the least conservative escapement policy (maximize harvest, $\theta = 1.0$).

Results more similar to ours were obtained by Swartzman et al. (1983) in simulation studies of the Pacific hake[2] *Merluccius productus* fishery. They compared the optimal constant effort policy to several "policy algorithms" in which harvest depended on an index of stock size. The intent of the policy algorithm was to fully exploit strong year classes but to protect the stock when in poor condition. Mean harvest under a constant effort policy was comparable to that obtained under the policy algorithms, and variability in harvest was considerably lower. The policy algorithms did maintain a higher catch per effort than did the constant effort policy, which illustrates that one cannot manage simultaneously for high yields, low variability in yield, and high catch per effort.

To better understand the relationship between different types of harvesting policies, we used simulation studies to compare alternative policies of the form

$$h = b_0 + b_1 S; \qquad (2)$$

that is, equation (1) with $b_0 = -\gamma\delta$, $b_1 = \gamma$, and $\theta = 1.0$ (Hilborn 1985). Following Hilborn (1985),

---

[2] Marketed as Pacific whiting.

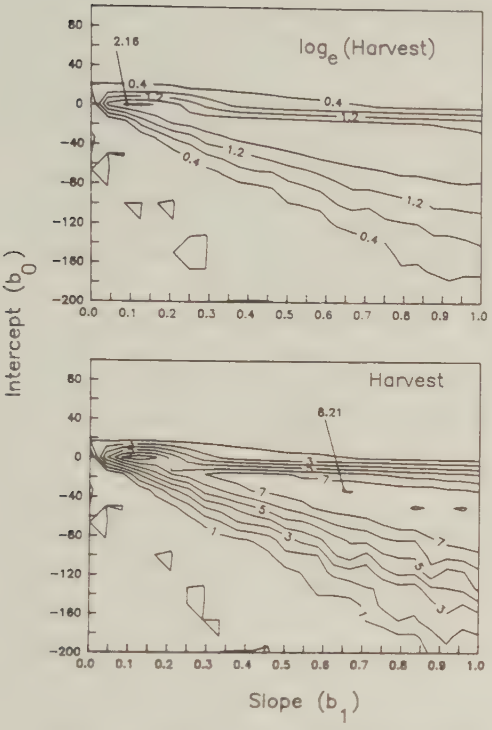


FIGURE 5.—Contour plots of average log$_e$(harvest) and harvest for widow rockfish based on the harvesting policy $h = b_0 + b_1S$, for which h and S represent harvest and stock biomass, respectively. Points 2.16 and 8.21 represent maximum values for average log$_e$(harvest) and harvest, respectively. These plots were obtained by assuming a natural mortality rate (M) of 0.15; results for M = 0.20 were similar and are not shown here.

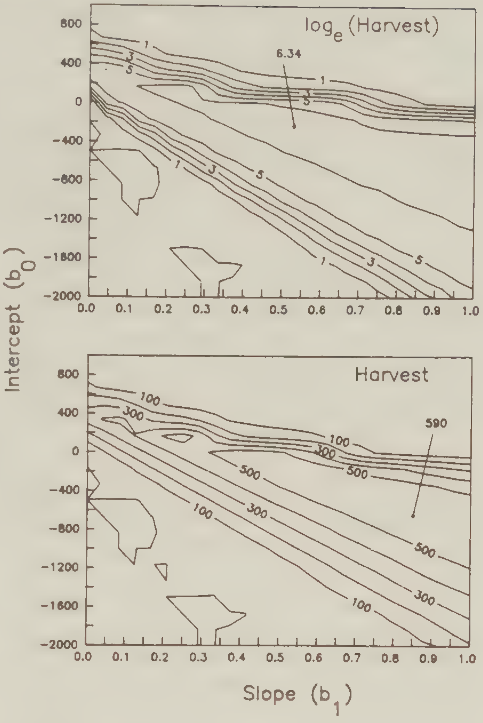


FIGURE 6.—Contour plots of average log$_e$(harvest) and harvest for Atlantic menhaden based on the harvesting policy $h = b_0 + b_1S$, where h and S represent harvest and stock biomass, respectively. Points 6.34 and 590 represent maximum values for average log$_e$(harvest) and harvest, respectively.

we used total stock biomass as S and examined a grid of policies for $b_0 = -S_{\max}$ to $S_{\max}$ and b_1 = 0.0 to 1.0. We obtained an estimate of $S_{\max}$, the equilibrium stock biomass in the absence of fishing, from a deterministic model using the estimate of expected recruitment described earlier. As was the case for equation (1), there are several policies of special interest: constant catch ($b_1 = 0$, $b_0 > 0$); approximately constant effort ($b_0 = 0$); and constant escapement ($b_1 = 1$, $b_0 < 0$) (Hilborn 1985).

By plotting contours for average harvest or log harvest, the relative performance of alternative types of policies can readily be seen (Hilborn 1985). Each contour plot in Figures 5 and 6 represents a grid of 625 policies that was obtained by varying both b_0 and b_1 over 25 evenly spaced levels. For each policy, an estimate of mean harvest and mean log harvest was obtained from 10 replicate simulation runs, each of which was 5λ years in length. In the region about the optimum, we used 100 replicates per point to obtain a smoother surface, but found, as did Hilborn (1985), that the results were essentially equivalent to those from 10 replicates. Our results also indicated that, if the only objective was to locate those policies that maximized harvest or log harvest, the search could have been restricted to the set of policies where

$$b_0 + b_1\,(1.5S_{\text{msy}}) > 0, \text{ and}$$
$$b_0 + b_1\,(0.5S_{\text{msy}}) < S_{\text{msy}}.$$

This range was obtained by assuming that the optimal stock size would be ±50% of S_{msy} and that the equilibrium harvest under that policy would be greater than 0 but less than S_{msy}. Substantial computational effort can be saved by restricting the search to this region, although less information would be obtained about suboptimal policies. Reducing computational effort is worthwhile when microcomputers are used because about 21 h were required to calculate all 625 points when 10 replicates per point were used.

The harvest-maximizing policy for widow rockfish was neither a constant effort nor constant escapement policy, but rather an intermediate form (Figure 5). When log harvest was plotted, the peak of the response surface shifted away from constant escapement policies, and the policy that maximized log harvest was a constant effort policy. These results are in general agreement with the more refined estimates obtained in the optimization studies. Mean harvest was similar although the best policies from the contour plots were slightly inferior (about 2%) to those obtained in the optimization studies.

For comparison, we also simulated the Atlantic menhaden fishery, using a simpler model (Hightower and Grossman 1985) than that used by Ruppert et al. (1985). We found that the harvest-maximizing policy for Atlantic menhaden was more similar to a constant escapement policy than was the policy for widow rockfish (Figure 6). This is a reasonable result because our Atlantic menhaden model incorporated a dome-shaped (Ricker) spawner–recruit relationship, whereas the widow rockfish model used a weak Beverton–Holt relationship. When a dome-shaped curve is used, the optimal policy may be to maintain constant escapement in order to produce a particular level of recruitment. There would be less incentive for maintaining a constant stock size when a Beverton–Holt curve is used. Using a simpler population model, Deriso (1985) suggested that constant effort policies maximize log harvest except in cases where the recruitment curve is dome-shaped. The policy that maximized log harvest for Atlantic menhaden was intermediate in form (Figure 6). It should be noted, however, that differences in performance were less than 1% among constant effort, constant escapement, and intermediate policies.

Results from the contour plots and optimization studies both showed that, for widow rockfish, the two-parameter harvesting policies (equation 1 with θ fixed or equation 2) provided only a negligible increase in mean harvest over the simpler constant effort policies. Furthermore, the increase in harvest would be accompanied by a much greater proportional increase in the variability of harvest. We also failed to detect any increase in harvest for Atlantic menhaden, although our model differed in several respects from the model used by Ruppert et al. (1985). They used a Beverton–Holt spawner–recruit relationship and a different error term, as well as density-dependent functions for both weight and fecundity. These results suggest that improvement in harvest may depend on model formulation or, ultimately, on how accurately the model represents the fishery. For stocks where density dependence is not strong, we suggest that only minor improvement will be gained through the use of two-parameter harvesting policies.

Acknowledgments

We thank D. Ruppert and W. Getz for comments on the manuscript.

References

Barss, W. H., and T. W. Echeverria. 1987. Maturity of widow rockfish *Sebastes entomelas* from the northeastern Pacific 1977–1982. NOAA (National Oceanic and Atmospheric Administration) Technical Report NMFS (National Marine Fisheries Service) 48:13–18.

Deriso, R. 1985. Risk adverse harvesting strategies. Lecture Notes in Biomathematics 61:65–73.

Dew, P. M., and K. R. James. 1983. Introduction to numerical computation in Pascal. Springer-Verlag, New York.

Getz, W. M. 1985. Optimal and feedback strategies for managing multicohort populations. Journal of Optimization Theory and Applications 46:505–514.

Gunderson, D. R. 1984. The great widow rockfish hunt of 1980–1982. North American Journal of Fisheries Management 4:465–468.

Hennemuth, R. C. 1979. Man as predator. Pages 507–532 *in* G. P. Patil and M. L. Rosenzweig, editors. Contemporary quantitative ecology and related ecometrics. International Cooperative Publishing House, Fairland, Maryland.

Hightower, J. E., and G. D. Grossman. 1985. Comparison of constant effort harvest policies for fish stocks with variable recruitment. Canadian Journal of Fisheries and Aquatic Sciences 42:982–988.

Hilborn, R. 1985. A comparison of harvest policies for mixed stock fisheries. Lecture Notes in Biomathematics 61:75–87.

Hogg, R. V., and A. T. Craig. 1978. Introduction to mathematical statistics, 4th edition. Macmillan, New York.

Kiefer, J., and J. Wolfowitz. 1952. Stochastic estimation of the maximum of a regression function. Annals of Mathematical Statistics 23:462–466.

Law, A. M., and W. D. Kelton. 1982. Simulation modeling and analysis. McGraw-Hill, New York.

Lenarz, W. H. 1987. Ageing and growth of widow rockfish. NOAA (National Oceanic and Atmospheric Administration) Technical Report NMFS (National Marine Fisheries Service) 48:31–35.

Mendelssohn, R. 1982. Discount factors and risk aversion in managing random fish populations. Canadian Journal of Fisheries and Aquatic Sciences 39:1252–1257.

Murphy, G. 1965. A solution of the catch equation. Journal of the Fisheries Research Board of Canada 22:191–202.

PFMC (Pacific Fishery Management Council). 1982. Final fishery management plan and supplemental environmental impact statement for the Washington, Oregon, and California groundfish fishery. PFMC, Portland, Oregon.

PFMC (Pacific Fishery Management Council). 1985. Status of the Pacific Coast groundfish fishery through 1985 and recommended acceptable biological catches for 1986. PFMC, Portland, Oregon.

Ruppert, D., R. L. Reish, R. B. Deriso, and R. J. Carroll. 1984. Optimization using stochastic approximation and Monte Carlo simulation (with application to harvesting of Atlantic menhaden). Biometrics 40:535–545.

Ruppert, D., R. L. Reish, R. B. Deriso, and R. J. Carroll. 1985. A stochastic population model for managing the Atlantic menhaden (*Brevoortia tyrannus*) fishery and assessing managerial risks. Canadian Journal of Fisheries and Aquatic Sciences 42:1371–1379.

Swartzman, G. L., W. M. Getz, R. C. Francis, R. T. Haar, and K. Rose. 1983. A management analysis of the Pacific whiting (*Merluccius productus*) fishery using an age-structured stochastic recruitment model. Canadian Journal of Fisheries and Aquatic Sciences 40:524–539.

Ueber, E. 1987. Widow rockfish fishery. NOAA (National Oceanic and Atmospheric Administration) Technical Report NMFS (National Marine Fisheries Service) 48:53–56.

American Fisheris Society Symposium 6:209–210, 1989

Using GENMOD to Develop Harvesting Policies for Multiaged Fish Stocks

JOSEPH E. HIGHTOWER AND WILLIAM H. LENARZ

Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service
3150 Paradise Drive, Tiburon, California 94920, USA

Abstract.—Program GENMOD is a microcomputer-based simulation program that applies an age-structured population model to problems of optimal harvesting policy. It can be used to explore alternative harvesting policies and determine the policy that best satisfies conflicting objectives of fishery management. This public-domain program is written for IBM PC and PC-compatible systems.

The GENMOD microcomputer program links a generalized age-structured population model with an optimization routine. The program can be used to obtain optimal harvesting policies for a range of management objectives, including maximization of harvest and minimization of variability about a target harvest, stock biomass, or spawning stock. The program also can be used to simulate the behavior of the fishery when either optimal or suboptimal policies are implemented. For each policy examined, the program provides a time series of estimates of stock size, fishing mortality, and yield that can be used to determine if the stock would be maintained at or restored to an appropriate level, if yield would deviate unacceptably from historical levels, and if yield or fishing effort would vary unacceptably from year to year. The program is best used to explore alternative harvesting policies in order to determine which policy best satisfies the conflicting objectives encountered in managing a fishery. It is written in Turbo Pascal for use with IBM PC and PC-compatible systems. Copies of the program and documentation can be obtained from the American Fisheries Society Computer Users Section library.

The model is a slightly generalized version of a deterministic model presented by Getz (1980). Models of this form frequently are used in conjunction with cohort analysis to analyze historical catch data and to develop recommendations for future harvests. The model can be used for stocks with up to 30 age-classes, and natural mortality, catchability, weight, and fecundity can vary by age. Males and females are pooled, however, so sex-specific differences in growth or mortality should not be large if this model is used. The spawner–recruit relationship can be represented by a constant or by a Ricker or Beverton–Holt curve, and spawning can occur either before or after a fishing season of variable length. The model should be useful for a wide range of single-species fisheries, as long as a single gear type is used to harvest the stock.

Program Options

Optimization

The first optimization routine is used to determine the levels of fishing effort that maximize (or minimize) a specific objective function over an *N*-year planning horizon. This is a deterministic approach; therefore, random variability in recruitment is not considered. The routine can be used to predict the expected outcome of implementing alternative optimal harvesting policies; for example, policies for rehabilitating overexploited stocks (Hightower and Grossman 1987). The following objective functions can be used: (1) maximize harvest; (2) maximize log(harvest + 1); (3) minimize the squared difference between annual harvests and a target harvest; (4) minimize the squared difference between stock biomass at the end of each fishing season and a target stock biomass; and (5) minimize the squared difference between the spawning stock at the end of each fishing season and a target spawning stock. An end-point penalty can be used to force the stock to converge on a desired end point; otherwise, the final status of the stock is not considered. Under a harvest-maximizing policy, stock depletion will occur unless an end point is used.

The second optimization routine is used to develop harvesting policies of the type proposed by Ruppert et al. (1984, 1985), in which harvest is either a linear or nonlinear function of stock size. These policies are obtained from a stochastic model and would be appropriate, therefore, for stocks in which year-class strength varies widely (Hightower and Lenarz 1989, this volume).

Simulation

The simulation routine is used to examine the short- and long-term behavior of the model when recruitment is assumed to be a random variable. This routine can be used to evaluate the performance of policies developed in the optimization routines, or to compare those routines with suboptimal alternatives. The program will estimate the steady-stage mean and variance or the frequency distribution for yield, spawning stock, or recruitment. For a more detailed examination of model behavior, a short-term option can be used to produce annual estimates of yield, spawning stock, and the number-at-age vector.

References

Getz, W. M. 1980. Harvesting models and stock recruitment curves in fisheries management. Pages 284–304 *in* W. M. Getz, editor. Mathematical modelling in biology and ecology. Springer-Verlag, Berlin.

Hightower, J. E., and G. D. Grossman. 1987. Optimal policies for rehabilitation of overexploited fish stocks using a deterministic model. Canadian Journal of Fisheries and Aquatic Sciences 44:803–810.

Hightower, J. E., and W. H. Lenarz. 1989. Optimal harvesting policies for the widow rockfish fishery. American Fisheries Society Symposium 6:83–91.

Ruppert, D., R. L. Reish, R. B. Deriso, and R. J. Carroll. 1984. Optimization using stochastic approximation and Monte Carlo simulation (with application to harvesting of Atlantic menhaden). Biometrics 40:535–545.

Ruppert, D., R. L. Reish, R. B. Deriso, and R. J. Carroll. 1985. A stochastic population model for managing the Atlantic menhaden *(Brevoortia tyrannus)* fishery and assessing managerial risks. Canadian Journal of Fisheries and Aquatic Sciences 42:1371–1379.

8925

Predation on Ocean Krill

In developing the hypothesis that "high-density demersal layers" of krill (*Meganyctiphanes norvegica*) at the bottom of submarine canyons are a major prey of fishes on Georges Bank, Greene *et al.* (*1*) may be missing a major facet of the trophic interactions among these organisms. According to their hypothesis, the fishes make descents into deep water next to the Bank, where, it is suggested, there is advantage in feeding on these vertical migrators when they are in their normal daytime aggregations. But this is not how the interactions proceed in what probably are similar situations elsewhere.

It has been widely reported (*2–4*) that fishes which inhabit relatively shallow banks or shelves feed heavily by day on organisms that, like *M. norvegica*, make extensive diel vertical migrations in adjacent deep water. The reports have come from the continental shelves of North America (*2*) and Australia (*3*), as well as from a central Pacific atoll (*4*); and in addition to various species of krill, the vertically migrating prey have included copepods and myctophid fishes. In the reported cases, however, the predatory fishes do not descend from the shelf or bank into the adjacent depths to take prey from the concentrations that form there by day. Rather, they feed on individuals that, after having been carried by currents (or swimming) over the shelf-bank while in the surface waters at night, are trapped by the relatively shallow shelf-bank when in the morning they descend toward their normal daytime depths. Apparently these organisms are especially vulnerable to predators in this setting, which is very different from their normal daytime habitat.

Edmund S. Hobson
Southwest Fisheries Center,
Tiburon Laboratory,
3150 Paradise Drive,
Tiburon, CA 94920

REFERENCES

1. C. H. Greene, P. H. Weibe, J. Burczynski, M. J Youngbluth, *Science* **241**, 359 (1988)
2. J. D. Isaacs and R. A. Schwartzlose, *ibid* **150**, 1810 (1965); W. T. Pereyra, W. G. Pearcy, F. E. Garvey, *J Fish Res Board Can* **26**, 2214 (1969); R Brodeur and W. G. Pearcy, *Fish Bull U.S* **28**, 289 (1984); J. R. Chess, S. E. Smith, P. C. Fisher, *Calif Coop Oceanic Fish Invest Rep.*, in press.
3. T. A. Clarke, *Copeia* 605 (1984)
4. E. S. Hobson and J. R. Chess, *Pacific Sci.* **40**, 24 (1986)

12 August 1988; accepted 16 September 1988

Response: In our paper (*1*), we hypothesized that squid and demersal fish production attributed to Georges Bank might be subsidized by the exploitation of krill from the submarine canyons and other deep waters surrounding the Bank. At present, the evidence for such a subsidy is circumstantial; krill are an important but variable dietary component of the Bank's commercially important squid and demersal fish stocks, and many of these stocks seasonally move off the Bank (as defined by the 200-meter isobath) into the surrounding deep waters where the high-density krill demersal layers are found. Unfortunately, little is known about the behavior and diets of these species when they move into deeper water. As we stated, closer examination of the spatial and temporal coupling between predator and prey populations will be essential to determine the validity of our hypothesis.

Hobson (*2*) raises a valid point with regard to the spatio-temporal coupling between predator and prey populations. If krill are the missing link in the Georges Bank food chain, then they must move onto the Bank either through vertical migration and advection by currents (or active swimming), as Hobson suggests, or the squid and fish stocks must descend into deeper water and feed, as we implied. Initially, we favored the mechanism hypothesized by Hobson, since there is ample evidence for such events occurring on other banks (*3*) and seamounts (*4*) around the world. However, extensive zooplankton and micronekton surveys on Georges Bank (*5*) indicate that krill rarely intrude on the shallower portions of the Bank, and thus the circumstantial evidence for Hobson's hypothesis does not appear to exist. On the other hand, fishery surveys on and around Georges Bank (*6*) indicate that many squid and demersal fish stocks move off the Bank seasonally into the deeper waters, where high-density krill demersal layers have been observed. Therefore, we chose to emphasize the latter hypothesized mechanism for the trophic linkage rather than the one Hobson suggests. So little is known that neither hypothesis should be given preference. A considerable amount of work by oceanographers and fishery scientists must be done before the role of krill in the Georges Bank food chain can be fully appreciated.

CHARLES H. GREENE
Ecosystems Research Center,
Corson Hall,
Cornell University,
Ithaca, NY 14853
PETER H. WIEBE
Biology Department,
Woods Hole Oceanographic Institution,
Woods Hole, MA 02543

REFERENCES

1. C. H. Greene, P. H. Wiebe, J. Burczynski, M. J. Youngbluth, *Science* **241**, 359 (1988).
2. E. S. Hobson, *ibid*
3. J. D. Isaacs and R. A. Schwartzlose, *ibid* **150**, 1810 (1965); A. Genin, L. Haury, P. Greenblatt, *Deep-Sea Res.* **35**, 151 (1988).
4. G. W. Boehlert and A. Genin, in *Sea Mounts, Islands, and Atolls*, B. H. Keating, P. Fryer, R. Batiza, G. Boehlert, Eds. (American Geophysical Union, Washington, DC, 1987), pp. 319–334.
5. C. S. Davis, in *Georges Bank*, R. H. Backus and D. W. Bourne, Eds. (MIT Press, Cambridge, MA, 1987), pp. 256–267; K. Sherman *et al.*, in *ibid.*, pp. 268–282.
6. T. R. Azarovitz and M. D. Grosslein, in *ibid.*, pp. 315–346; B. E. Brown, in *ibid.*, pp. 480–493

9 September 1988; accepted 16 September 1988

8926

REPRINT FROM
Calif. Fish and Game 75(3): 169–183 1989

NOTES

MASS STRANDINGS OF JUVENILE SHORTBELLY ROCKFISH AND PACIFIC HAKE ALONG THE COAST OF NORTHERN CALIFORNIA

Carcasses of young-of-the-year (YOY) shortbelly rockfish, *Sebastes jordani*, and Pacific hake, *Merluccius productus*, littered shores of northern California during June 1988. These strandings caused much concern among observers, but there was little understanding of why they occurred (Klineman 1988). Here we discuss our observations on these and other occurrences during recent years, and draw some conclusions.

At the same time that carcasses littered the beaches, we observed large schools of YOY shortbellies, many in poor condition, during underwater surveys (scuba) near shore along the Sonoma and Mendocino coasts. These were unusual occurrences. Although YOY shortbellies have dominated samples taken offshore by midwater trawl (Peter Adams, National Marine Fisheries Service, Tiburon Laboratory, unpubl. data) we have seen them only occasionally during hundreds of hours of observations near shore over the past 10 years.

The YOY shortbelly schools were most dense right up against rocky shores, where many filled the water from surface to bottom. Virtually every member of these shortline schools was marked by lacerations and/or abrasions, and moribund individuals were common. There were many dead YOY shortbellies on the bottom beneath the schools, and among them lay numerous dead hake. The hake, too, were lacerated and abraded, and, while no living individuals were seen (we have never seen living hake in this habitat), it was clear they had been feeding on the YOY shortbellies. The abdomens of most were greatly distended, and stomachs gorged with YOY shortbellies protruded from the partially decomposed bodies of some (Figure 1).

Probably it is normal that hake prey heavily on YOY shortbellies at this time of year, as do salmon and other coastal predators (Merkel 1957, Lenarz 1980, Chess et al. 1988). We assume that these encounters usually occur offshore above the continental shelf and slope, since that is where hake ordinarily feed (Alverson and Larkins 1969, Gotshall 1969). In fact, hake and YOY shortbellies may be ill-suited to shoreline interactions as predator and prey. Certainly feeding-related behaviors that are adaptive in open water can be maladaptive in confined surroundings. In particular, the explosive, straightforward charge typical of open-water predators, as well as the radiating, evasive response to such attacks typical of schooling prey, are risky maneuvers among rocks or at the water's edge. It is known, for example, that when schools of small fish are driven against the shoreline by large, active predators, subsequent actions often carry both predator and prey onto the beach (Hobson 1968).

The difficulties of maneuvering in confined space would be especially great at night, when visibility is reduced, and we believe that this is when the shortbellies were attacked. Being nocturnal predators (Hart 1973), hake should function well in dim light. However, their night-feeding normally occurs in obstruction-free surface waters offshore (Alton and Nelson 1970, Livingston 1983), where there is no danger of stranding or of colliding with abrasive surfaces. We suggest that it was the inability of YOY shortbellies and hake to accommodate their behaviors to these dangers in the obstruction-filled waters near shore that resulted in the recently observed mortalities.

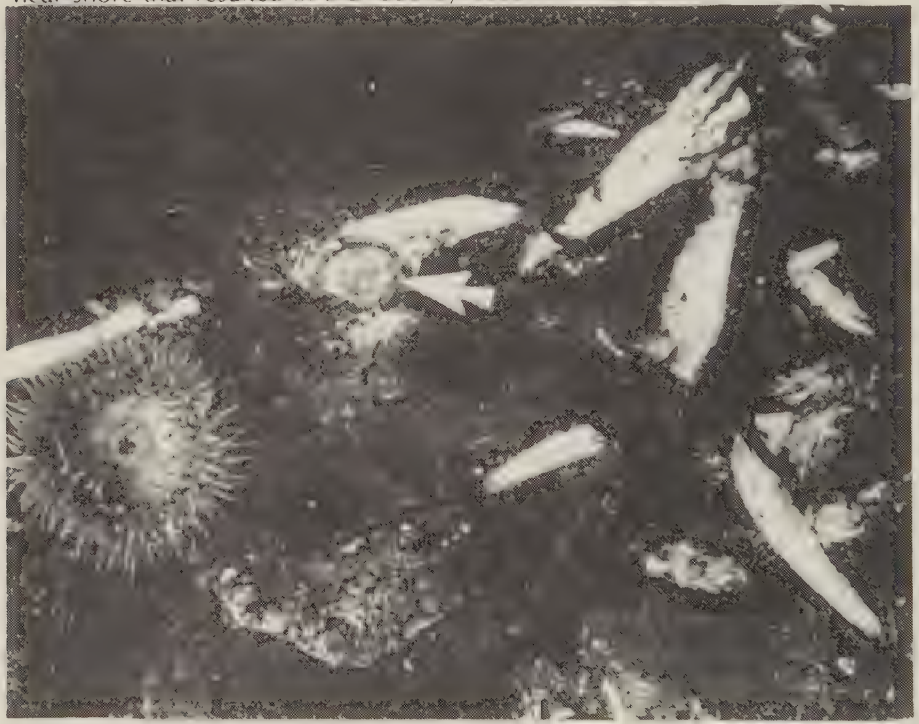


FIGURE 1. Carcasses of hake and shortbelly rockfish on the seabed beneath a shoreline YOY shortbelly school on the Sonoma coast. Arrow points to stomach gorged with YOY shortbellies (readily identifiable through the distended stomach wall) protruding from the decomposed body of a hake.

The acute stress evident in the YOY shortbellies and hake was in sharp contrast with the healthy condition evident in nearby members of the nearshore community. The neighboring residents included YOY of several *Sebastes* species, most notably blue rockfish, *S. mystinus*, black rockfish, *S. melanops*, and yellowtail rockfish, *S. flavidus*. These YOY rockfishes were numerous over most of the nearshore habitat, but, unlike the YOY shortbellies, they were not concentrated at the shoreline. Furthermore, we saw none that appeared in poor condition, none among the carcasses on shore, and none in the stomachs of hake. In fact, we have no evidence they were in any way stressed, which supports our conclusion that the problems suffered by the YOY shortbellies and hake resulted from being maladapted to nearshore conditions, not from problems suffered by the nearshore environment.

While it may be that the hake entered the nearshore habitat to feed on the YOY shortbellies, this still leaves us to question why the YOY shortbellies were there. That the strandings occurred during June follows from this being a time of year when YOY shortbellies are particularly abundant off northern California (unpublished data from midwater-trawl surveys, Peter Adams, Tiburon Laboratory). But since these fish usually are some distance offshore, why during early June of 1988 were so many close enough inshore to become stranded?

The answer may involve the wind. The strong northerlies that prevail in this region during spring and summer drive the coastal surface waters seaward (Ekman 1904, Bakun 1973), and this acts to keep the YOY shortbellies offshore. But during the month before the strandings short periods of weaker-than-usual northerlies alternated with short periods of southerlies. And on the days immediately before and during our first observations of YOY shortbellies near shore, the wind was from the south at up to 14 knots (Figure 2). Sea temperatures near shore increased sharply at this time, indicating that the surface flow had turned toward the coast (Hobson and Chess 1988), and we believe that this is what brought the YOY shortbellies to the shore.

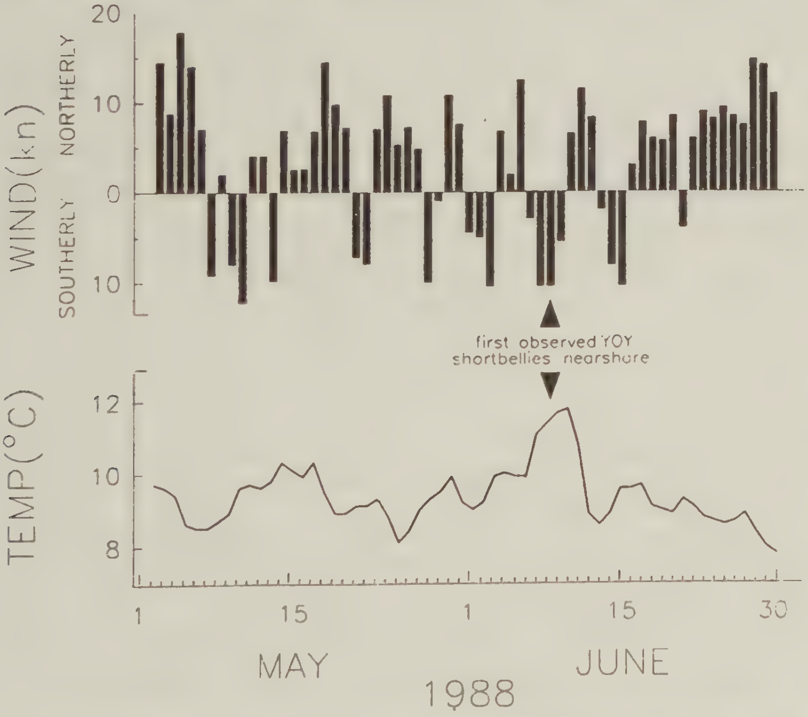


FIGURE 2. Relation between wind and sea temperatures nearshore off the Mendocino coast during May and June, 1988.

Plotted wind values are averages of 2–5 daily readings from the NOAA weather station at Mendocino. Southerly values represent winds from south of east-west axis, northerly values represent winds from north of this axis. *Plotted sea temperatures* are daily means of 72 readings of a digital recording thermometer placed at a depth of 10m in the nearshore habitat.

Previous nearshore occurrences of YOY shortbellies support this hypothesis. Only twice before during the past 10 yr of extensive work in these habitats have we seen large schools of YOY shortbellies close to shore, and both times (early

July 1982 and early June 1985) were similarly marked by southerly winds and abruptly elevated sea temperatures (E. Hobson, Tiburon Laboratory, unpubl. data). We are unaware of strandings during the 1982 episode, but in 1985 we saw YOY shortbellies stranded on the Marin coast, and received reports from fishermen of juvenile shortbellies and hake being stranded along the Mendocino coast. There also were widespread strandings of YOY shortbellies and hake along the Mendocino and Sonoma coasts during late June 1987 (Peter Kalvass, California Department of Fish and Game, pers. comm.), and while we lack wind data for that period (the weather station was closed that week), our thermograph record of sharply elevated sea temperatures indicates that these strandings occurred during an episode of shoreward surface transport. On the other hand, over this same 10-yr period there have been episodes of strong shoreward transport during June–July when no YOY shortbellies were seen near shore, so apparently there are other variables involved.

One of these other variables is likely to be the relative number of YOY shortbellies offshore, and this number differs greatly from year to year with the success of recruitment. Annual assessments of recruitment in this species, based on occurrences of YOY in the gut contents of king salmon, *Oncorhynchus tshawytscha*, have been made since 1980 by Peter Adams and Wayne Samiere, of the Tiburon Laboratory. Significantly, their unpublished results indicate strong recruitment during the four years that YOY shortbellies were noted by us or others to be unusually abundant near shore. Furthermore, their data indicate relatively weak recruitment during the other six years, which may explain why occasional periods of strong shoreward transport during June–July of those years did not, to our knowledge, bring YOY shortbellies near shore.

LITERATURE CITED

Alton, M. S. and M. O. Nelson. 1970. Food of the Pacific hake, *Merluccius productus,* in Washington and northern Oregon coastal waters. U. S. Fish Wildl., Circ. 332:35–42.

Alverson, D. L. and H. A. Larkins. 1969. Status of knowledge of the Pacific hake resource. CalCOFI Rept., 13:24–31.

Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946–71. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF 671, 103p.

Chess, J. R., S. E. Smith, and P. F. Fischer. 1988. Trophic Relationships of the shortbelly rockfish, *Sebastes jordani,* off central California. CalCOFI Rept., 29:129–136.

Ekman, V. W. 1904. On the influence of the earth's rotation on ocean currents. Ark. Mat. Astron. Fys., 2, 11:1–52.

Gotshall, D. W. 1969. Stomach contents of Pacific hake and arrowtooth flounder from northern California. Calif. Fish and Game, 55:75–82.

Hart, J. L. 1973. Pacific fishes of Canada. Fish. Res. Bd. Canada, Bull. 180, 740p.

Hobson, E. S. 1968. Predatory behavior in some shore fishes in the Gulf of California. Bur. Sport Fish Wildl. Res. Rpt. 98, 92p.

________, and J. R. Chess. 1988. Trophic relations of the blue rockfish, *Sebastes mystinus,* in a coastal upwelling system off northern California. Fish. Bull., 86:715–743.

Klineman, E. 1988. Thousands of fish die mysteriously along coast. The Press Democrat, Santa Rosa, Calif. 18 June, p.1.

Lenarz, W. H. 1980. Shortbelly rockfish, *Sebastes jordani*: a large unfished resource in waters off California. Mar. Fish. Rev., 42:34–40.

Livingston, P A. 1983. Food habits of Pacific whiting, *Merluccius productus,* off the west coast of North America, 1967 and 1980. Fish. Bull., 81:629–636.

Merkel, T. J. 1957. Food habits of the king salmon, *Onchorhynchus tshawytscha* (Walbaum), in the vicinity of San Francisco, California. Calif. Fish and Game, 43:249–270.

—Edmund S. Hobson and Daniel F. Howard, Southwest Fisheries Center, Tiburon Laboratory, 3150 Paradise Drive, Tiburon, CA 94940. Accepted for publication January 1989.

8927

MARINE MAMMAL SCIENCE, 5(4):315–342 (October 1989)
© 1989 by the Society for Marine Mammalogy

GROWTH LAYERS IN TEETH FROM KNOWN-AGE, FREE-RANGING BOTTLENOSE DOLPHINS

Aleta A. Hohn
Southwest Fisheries Center, National Marine Fisheries Service, P.O. Box 271,
La Jolla, California 92038

Michael D. Scott
Inter-American Tropical Tuna Commission, ℅ Scripps Institution of Oceanography,
La Jolla, California 92037

Randall S. Wells
University of California, Long Marine Laboratory, Santa Cruz, California 95060 and
Dolphin Biology Research Associates, 163 Siesta Drive,
Sarasota, Florida 34242

Jay C. Sweeney
A. Blair Irvine
Dolphin Biology Research Associates, 163 Siesta Drive,
Sarasota, Florida 34242

Abstract

Growth layers were examined in teeth collected from free-ranging bottlenose dolphins, *Tursiops truncatus,* from Florida that have been part of a long-term study begun in 1970; 26 of the dolphins were of known or approximately known age, and 19 were of minimum known age. A second tooth was extracted from 6 animals for examination of growth that had taken place in the interval following the initial extraction. The teeth were read for age estimates without knowledge of any data pertaining to the animals. Most of the estimated ages were the same as or close to the known and approximately known ages of the animals, ranging from 2 to 16 yr. We conclude that the structures we define as dentinal growth layer groups (GLGs) are annual, we describe sources of error in age estimates, and we provide a description of the GLG pattern that can be used by others to estimate age for dolphins.

Key words: age determination, growth layers, GLGs, teeth, *Tursiops truncatus,* bottlenose dolphin, known age, long-term studies.

The ability to estimate the age of individuals has been an important tool in the study of population biology. For most species of mammals, we have been able to count growth layers in teeth or bones to obtain age estimates. The use of these structures has generally been accepted and applied for age estimation even when they have not been calibrated for a species because (1) growth layers are very common, having been identified in most mammalian species examined, (2) the appearance and structure of growth layers have been similar among different species within similar tissues, such as teeth or bones, and (3) in each species for which data have been available, growth layers have been calibrated to real time showing the existence of annually occurring layers (see Klevezal' and Kleinenberg 1967, Grue and Jensen 1979).

Evidence for annual growth layers in teeth of dolphins has come primarily from bottlenose dolphins, *Tursiops truncatus,* especially those which were born in captivity or were captured young and spent the remainder of their lives in captivity (*e.g.,* Sergeant 1959, Sergeant *et al.* 1973, Hui 1980). When these animals died, their teeth were sectioned and dentinal growth layers were counted. The number of layers equalled the known age or approximated the suspected age of the dolphins and, thus, growth layers were interpreted to be annual. These interpretations have since been applied to non-captive animals, with the assumption that the annual layering patterns seen in teeth from captive dolphins pertain as well to dolphins in the wild.

A long-term study of a community of bottlenose dolphins on the west coast of Florida has provided the opportunity to calibrate age-estimation techniques on free-ranging, known-age dolphins. A large portion of this community of approximately 100 animals is identifiable through the use of tags, freeze brands, and natural marks (Irvine and Wells 1972; Irvine *et al.* 1981; Wells *et al.* 1980, 1987; Wells 1986). Tagging operations and surveys of the community were conducted periodically during 1970–1971, 1975–1976, and since 1980. A total of 91 individuals from the Sarasota dolphin community were captured, sexed, measured, and tagged during these periods, with many of these individuals being captured several times.

The long-term study has provided data for obtaining known or approximate ages of identifiable dolphins. The known-age dolphins are individuals which were observed as calves, newly born to identifiable mothers. In subsequent years, many of these calves were identified with their mothers and captured and marked for later re-identification. Approximately known-age animals are those for which, although the birth date was not known, a minimum or approximate age could be estimated on the basis of when the dolphin was first captured or identified from photographs as a naturally marked animal. For example, if an individual was captured while it was still a calf, the age could be estimated from length-at-age data. These data are available for specimens whose age and length are known and from growth curves (Harrison *et al.* 1972, Hohn 1980) and are precise for estimating age during the first 1–2 yr (Hohn and Hammond 1985). In some cases a maximum age could also be determined; for example, if an identifiable adult female was seen without a calf in the winter of 1980 and with a small calf in the summer of 1981, the age of the calf could be pinpointed to within a 6-mo period.

This relatively large, unique sample provides an opportunity for examining a number of questions regarding age estimation in dolphins. This study focuses on the following questions:

1. Can annual growth layers be identified in teeth from free-ranging, known-age bottlenose dolphins?
2. Do ages estimated from growth layers in teeth correspond to known ages?
3. Are there some individuals in which an obvious growth-layer pattern that matches the known or approximate age cannot be found?
4. Is it possible to identify one or more factors responsible for most of the error in age estimation?
5. Can the similarities and differences between the annual patterns be categorized to allow for the development of a written guide (or "model") to standardize age estimation from dolphin teeth?

The term *growth layer group* (GLG) has been used to describe the structures which comprise the repetitive layering pattern seen in dolphin teeth (Perrin and Myrick 1980). The amount of time represented by a GLG depends on how each investigator defines the repeating pattern being examined. Although GLGs do not automatically refer to annual layers, in this study we were interested in a repeating pattern (GLG) that represents one year's growth.

MATERIALS AND METHODS

Teeth were collected during eight field seasons (five summers and three winters) in 1984–1989, using extraction techniques described by Ridgway *et al.* (1975). Generally, tooth number 15 was taken from the lower left jaw. Teeth were collected from as many individuals as possible (19 in 1984, 15 in 1985, 9 in 1986, 4 during winter and 10 during summer in 1987, 1 during winter and 6 during summer in 1988, and 5 during winter in 1989). Of these specimens, 14 were of known age and 12 of approximately known age. For the rest, at most only a minimum age was known. From 6 animals, a second tooth was extracted in years following the initial extraction; 1 animal was of known age, 2 of approximately known age, and 3 of minimum or unknown age. Included in the sample were teeth from eight beach-cast specimens with no known history that stranded in the study area. Teeth extracted from live animals were randomly mixed with teeth from beach-cast specimens, and all field numbers were coded before processing.

The teeth were preserved in formalin for up to a month then stored in ethanol. The method for decalcifying, sectioning, staining, and mounting teeth is described in detail in Myrick *et al.* (1983) for teeth from *Stenella* spp. The only significant difference is that the smaller teeth from *Stenella* can be decalcified whole, while the larger teeth from *Tursiops* must be thick-sectioned first and these 2–3 mm sections then decalcified. The thick-sections were cut using an Isomet[1] low-speed saw with a diamond-embedded blade. Decalcification time using RDO[1], a commercially produced mixture of acids, ranged from 7–17 h, with the greater times required for older animals. Thin-sections were cut to 25 μm on a freezing microtome, stained in hematoxylin, and mounted in 100% glycerin.

---

[1] Reference to trade names does not imply endorsement by the authors' institutions.

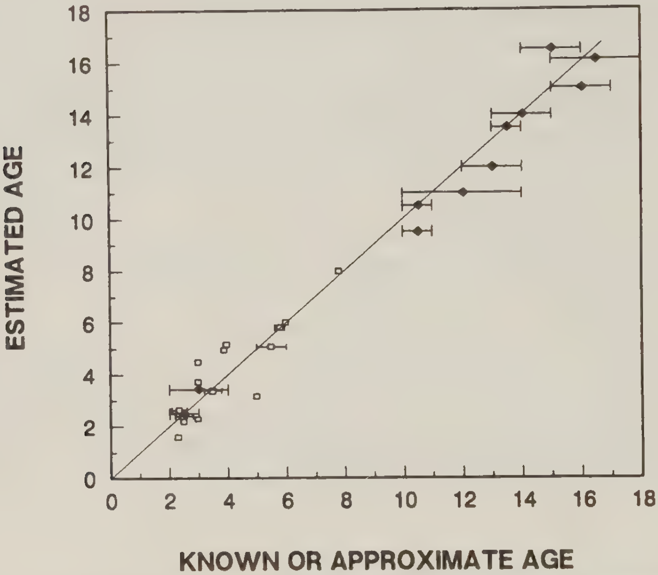


Figure 1. Relationship between the estimated ages and known or approximate ages of those animals for whom the age was known. The horizontal bars represent the range of ages possible for an individual (see Tables 1, 2, and 4). Squares represent known-age individuals and diamonds represent approximately known-age individuals. The line represents the one-to-one relationship between estimated and known age for comparison.

Age estimates were made without reference to collaborative data, such as age or length, or knowledge that a tooth represented the second extraction for the six individuals in which this occurred. There were two exceptions to this "blind" reading of tooth sections. Before the study began the tooth from one known-age animal was examined with knowledge of the animal's age to identify the annual layering pattern (No. 13). (A second tooth from this animal taken 2.5 yr later was read in the blind.) The other exception was for an animal from which a second tooth was collected after the animal was found beach-cast and the tooth prepared after other teeth from that season had been completed (No. 11). For the remaining specimens, age was estimated from counts of GLGs in both dentine and cement.

There were two components to the study. First, ages were estimated in the blind, as described above. These estimated ages were compared to the known or approximately known ages for examination of accuracy, or, in the event that age estimates were inaccurate, for possible explanations why they were inaccurate. Second, the tooth sections were examined again, this time with knowledge of the known ages of animals, for the purpose of demarcating and measuring probable GLGs in dentine. On the basis of the known ages, probable GLGs were marked on an 8″ × 10″ photographic print of the section. GLG-thickness measurements were taken simultaneously at the location where the GLG was marked on the photograph. The measurements were made using an ocular micrometer in a compound microscope at 100× with transmitted light.

Table 1. Ages and age estimates for 13 known-age, free-ranging bottlenose dolphins from which one tooth was extracted. Table 4 includes an additional known-age animal from which two teeth were extracted. All body lengths and known ages pertain to the date when the tooth was collected. For ID No. 6, the estimated age was thought to be one of two possibilities.

ID no.	Fig. no.	Sex	Body length (cm)	Date of birth (mo/yr)	Date of tooth collection (mo/d/yr)	Age (yr)	
						Known	Estimated
148	3	F	217	9/84	1/06/87	2.3	1.6
157		M	192	1/84–7/84	9/01/86	2.1–2.6	2.6
15	5	F	218	10/81–5/82	6/29/84	2.2–2.8	2.4[a]
142	4	F	204	7/84	1/06/87	2.5	2.2
12	2	M	214	10/80–5/81	6/21/84	3.2–3.8	3.4
144		F	213	7/84	6/23/87	3.0	4.5[a]
61		F	212	6/83–7/83	6/27/86	3.0	3.8
140	6	F	213	7/84	6/22/87	3.0	2.3
17		M	215	7/81–9/81	6/25/85	3.8–4.0	4.9–5.2[a]
67	8	M	226	7/83	6/26/87	4.0	5.2[a]
20	9	F	226	7/82	6/29/87	5.0	3.2
6		M	221	4/80–9/80	6/26/86	5.8–6.2	6.0, 12.0[a]
33	11	M	228	3/81–5/81	1/20/89	7.7–7.9	8

[a] Quality of preparation of the sections poor.

RESULTS

Comparison of estimated and known ages—Age was estimated for 26 individuals of known or approximately known age, from a second tooth from one of those individuals, and for 19 individuals of minimum-known age (Tables 1–2). For the known or approximately known sample, a regression line fitted to estimated age on known or approximately known age (using interval midpoints) did not differ significantly from a slope of 1.0 and an intercept of 0 (Fig. 1). Estimated ages for specimens where minimum-age data were available were consistent with those data (Table 3).

Of the 27 estimates from known- or approximately known-age animals, 15 were the same as or close to the known age or within the range of the approximately known age (Tables 1–2). The largest differences between known and estimated age for the other 12 estimates occurred in specimens 3–4 yr old. The direction of error was not systematic (biased), *i.e.*, in some cases the estimates were high and in others low. While two of seven estimates for animals in these age classes were accurate, four of the other five differed by 0.7–1.5 yr from the known age. With two exceptions, these represented the largest differences between known or approximately known and estimated age across all age classes.

For one of the two exceptions (No. 6), two estimates were given at the time the tooth was read because of the uncertainty of the accuracy of one reading over the other (this was not done for other specimens). One estimate was twice that of the other. The lower estimate (6 yr) was correct. Upon re-examination of this tooth section, the thickness of GLGs supported the lower estimate.

Table 2. Approximately known ages and age estimates for 10 free-ranging bottlenose dolphins from which one tooth was extracted. Table 4 includes two additional approximately known-age animals from which two teeth were extracted.

ID no.	Fig. no.	Sex	Body length (cm)	Age (yr) Approx.	Age (yr) Estimated	Data to support approximately known age[a]
147		F	209	2–3	2.5[b]	Born after 1982, tooth taken 1985
25	7	F	211	2–4	3.4	Calf 2 yr earlier
149	10	M	218	5–6	5.1	188 cm 3.5 yr earlier
38		M	246	10–14	11[b]	226 cm 9 yr earlier
30		M	219	12–13	12.3	149-cm calf 12.4 yr earlier
155	12	M	253	12–14	12.3	224 cm 9 yr earlier
14		F	245	13–15	14[b]	224 cm 10 yr earlier
49	13	M	258	14–16	16.5	210 cm 12 yr earlier
27		M	253	15–17	15[b]	185 cm 14 yr earlier
56		M	258	15–18	16.1[b]	221 cm 12 yr earlier

[a] The following length-at-age data were used to support age estimates: 115 cm at birth, 178 cm at 1 yr, and 205 cm at 2 yr (estimated from known-age and known-length animals in the sample, unpublished data, Harrison *et al.* 1972, and Hohn 1980).

[b] Quality of preparation of the sections poor.

Otherwise, the largest absolute difference between known and estimated age was 1.8 yr (known age = 5 yr) for a dolphin whose tooth was abnormal (No. 20, see below). In most cases, given the known ages, the errors and probable GLGs were easily identified (Figs. 2–17).

For three animals, we were unable to identify GLGs which corresponded to the known age. In general appearance, none of the teeth showed obvious differences from specimens in which probable GLGs could be identified. The tooth from one animal was well-prepared and when age was estimated from it, GLGs seemed easy to identify (No. 142, Fig. 4). When the known age of the animal was checked, however, GLGs with the same pattern seen in teeth from most of the other animals could not be found. The tooth from another animal was poorly prepared and contained calcium inclusions (No. 67, Fig. 8), although the latter, in themselves, may distort GLGs they do not prevent identification of GLGs (*e.g.*, see Figs. 12 and 15). In the tooth from a third animal (No. 144) the sections were the most poorly prepared of these three specimens. Although layers were visible, an obvious pattern that corresponded to the known age could not be identified. An additional tooth from this specimen may permit us to identify the GLGs.

In the teeth of three animals (Nos. 20, 61, and 140) and possibly in a fourth (No. 67) collected within a month of their known birth day (all in June or July), when one might expect that little if any dentine would have formed beyond the end of the recently completed GLG, there was an appreciable amount of dentine deposited after the supposed end of the just completed GLG (see Figs. 6, 8, and 9). The appearance of this dentine was not an anomaly resulting from poorly prepared (off-center) sections.

Table 3. Age estimates for 19 free-ranging bottlenose dolphins of minimum-known age. Includes only specimens for which there is a sufficient history to provide a reasonable check on the estimated age. Table 4 includes two additional animals from which a second tooth was extracted.

ID no.	Sex	Body length (cm)	Estimated age (yr)	Previous history of animals
21	F	233	6.4	Independent juvenile 4 yr earlier
146	M	245	7.8	235 cm previous yr
59	F	238	9.3	Independent from mother 6 yr earlier
90	M	231	13.5[a]	Independent from mother 6 yr earlier
37	M	251	13.5[a]	Adult-sized 7 yr earlier
4	F	256	14.5	240 cm 9 yr earlier
28	F	253	17	Adult-sized 10 yr earlier
9	F	252	20–32[a]	230 cm 10 yr earlier, calf born to her 3 yr earlier
8	F	235	21[a]	Adult-sized 8 yr earlier
5	F	242	24[a]	239 cm 16 yr earlier
7	F	252	24	Adult-sized 15 yr earlier
73	M	276	25[a]	256 cm 15 yr earlier
34	M	273	26[a]	Adult-sized 5 yr earlier
16	F	248	27	247 cm 9 yr earlier
42	F	253	31	249 cm, with calf, 11 yr earlier
10	F	260	31[a]	256 cm, with calf, 9 yr earlier
40	M	271	33	Adult-sized 11 yr earlier
22	F	251	42[a]	250 cm, with calf, 10 yr earlier
1	F	252	44	250 cm, with calf, 10 yr earlier

[a] Quality of preparation of the tooth sections poor.

One animal in the sample (No. 30) was very small for its age and blood samples showed that it was anemic. It remained with its mother until it was 10 yr old. The tooth showed no signs of any irregularity, despite the abnormal growth rate in body length. It would not have been possible to determine the abnormal condition of the animal from its dentinal growth layers.

There was one anomalous tooth in which the pulp cavity was enlarged at the tip and the GLGs in this region were compressed (No. 20, Fig. 9), resulting in an underestimate of age. The tooth was taken from a known-age, apparently healthy animal. It was for this animal that the greatest difference between estimated and known age was obtained (1.8 yr).

Multiple extractions—For the six animals from which a second tooth was extracted, the time between extractions ranged from 3 mo to 3 yr (Table 4). The number of GLGs in blind counts matched the time between extractions for the animals. When the age estimated from one extraction did not match the approximate age (Nos. 3 and 11), the error resulted from misidentification of early-deposited GLGs rather than those deposited in the years between extractions. One exception to the above occurred in No. 154 because the GLGs were difficult to identify. The amount of dentine deposited during the time between extractions allowed us to identify probable GLGs.

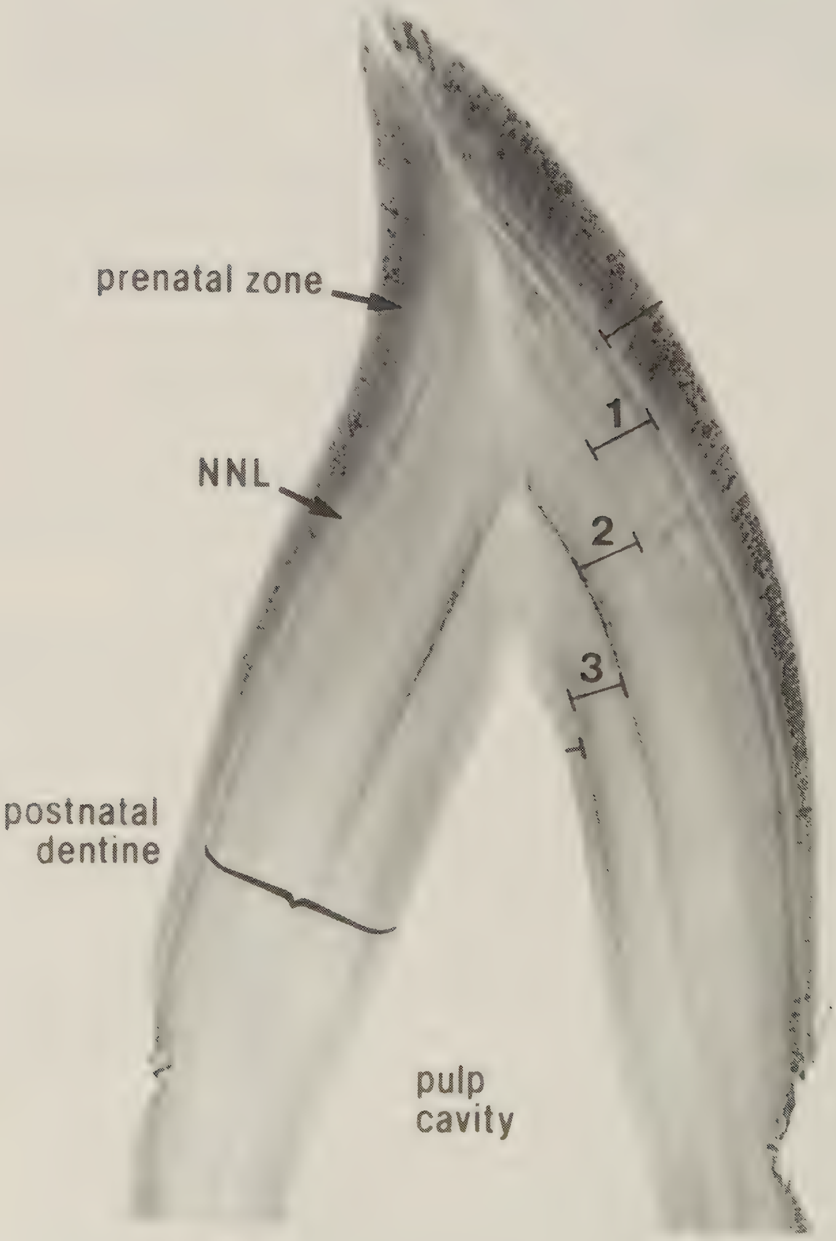


Figure 2. A good section of a bottlenose dolphin tooth. The section was cut on the buccal-lingual, mid-longitudinal ("on-center") plane rather than oblique to that plane ("off-center"), evident because the apices of the layers are pointed rather than round. The neonatal line is well-defined, picking up little, if any, stain. Accessory layers are apparent but not disruptively conspicuous. The boundary layer between the first and second GLGs

The GLGs were easy to distinguish even in older animals in which the GLGs had become narrow (Figs. 14–17). The appearance of layers (GLG boundary layers as well as accessory layers) and of areas with different stainability was virtually identical (disregarding preparation variability) in the two teeth from each individual, except for the additional years' growth.

One specimen was found dead and slightly decomposed. Although external identifying marks in the specimen were no longer visible, tooth number 15 was missing from the left lower jaw and we were able to help identify the individual using the dentinal layering pattern as a "fingerprint."

Main sources of error in age estimates—The greatest absolute errors in all age classes were due to misinterpretation of layers and to poorly prepared sections, with the latter condition contributing greatly to the occurrence of the former. Misinterpretation occurred when prominent, narrow, stained layers (accessory layers, see Hohn, in press) or distinct boundaries between lightly and darkly stained zones within GLGs were erroneously taken to be boundary layers between GLGs (*e.g.*, Fig. 3). The errors in age estimation in 3–4-yr-old specimens may be the result of too few GLGs having been deposited for the annual pattern to be clear, yet enough dentine having been deposited to cause confusion between accessory layers and GLG boundary layers. Even in well-prepared sections, accessory layers could be quite prominent (*e.g.*, Figs. 7 and 13).

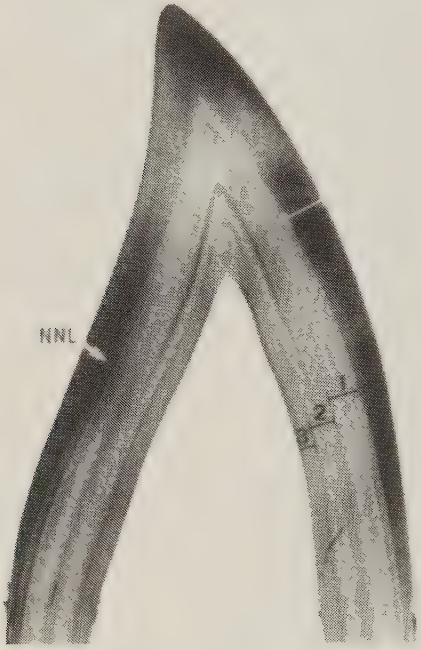
Poorly prepared sections most often influenced interpretation of layers when the orientation of the cut was other than mid-longitudinal along the buccal–lingual axis of the tooth. One difficulty in obtaining an on-center cut was that most of the teeth were curved in two directions, so that a cut that was on-center in one part of the tooth would be off-center somewhere else. A decision prior to cutting had to be made as to whether to minimize distortion near the tip of the tooth, which is more important for estimating age in younger animals, or near the pulp cavity, which may be more important for older animals. In some sections, probable GLGs could not be identified until we first determined the orientation of the cut.

When the cut was oblique to or laterally displaced from the mid-longitudinal axis ("off-center"), the GLGs were skewed, appearing wider than with a mid-longitudinal cut (because the layers are concentric, any orientation of cut other than through the center will produce a wider layer). The skewing accentuated the accessory layers, because they also become wider (*e.g.*, Figs. 5 and 14b). The skewing or widening was most evident in the first 2 GLGs. In addition,

---

←

is also not conspicuous, a condition common in many *Tursiops* and other delphinid teeth. The subsequent boundary layers between GLGs are well-defined. This tooth is from a male (No. 12) known to be 3.2-3.8 years old when the tooth was extracted. Symbols: NNL—neonatal line, numbers—GLG number, where the GLGs defined represent one year's growth. The bars in the postnatal dentine mark likely GLGs. The bar in the prenatal dentine marks the region at which the thickness of the prenatal zone was measured to use as a guide for identifying the first GLG (see Appendix). For GLG-thickness measurements see Table 5. The indentations on the lower, outer edges of the section occurred during tooth extraction.



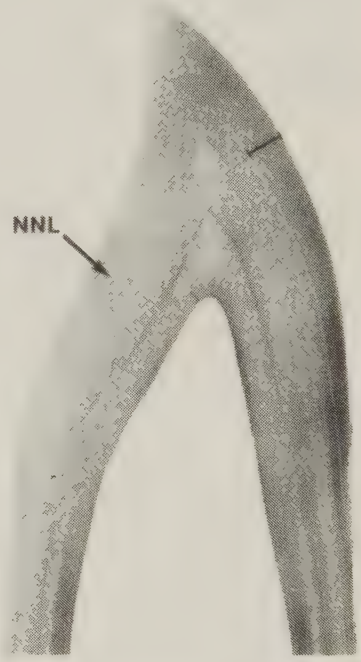
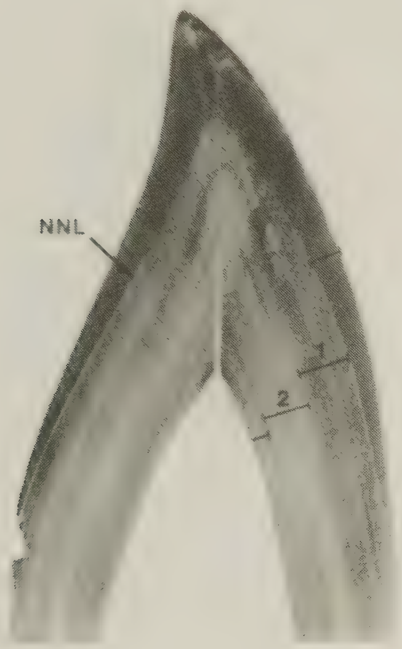


Figure 3. Tooth section from a known-age, 2.3-yr-old female (No. 148). The boundary layer between GLGs 1 and 2 is unusually well-defined for this sample of bottlenose dolphins. A very distinct accessory layer appears near the center of the second GLG. See Figure 2 for explanation of symbols and Table 5 for GLG-thickness measurements.

Figure 4. Tooth section from a known-age, 2.5-yr-old female (No. 142). No GLGs were marked in this section because the correct GLGs were not obvious (although 2.5 GLG-type layers can be seen, viewed from the edge of the pulp cavity towards the neonatal line). It is possible that in this animal, born in July, the distinctive layers were deposited during the winter, 6 mo out of phase with the time of birth (see text for discussion). See Figure 2 for explanation of symbols.

in GLGs cut obliquely the upper portion (near the apices) appears concave rather than, as in mid-longitudinal buccal-lingual sections, straight or slightly convex on the convex side of the tip of the tooth and slightly concave on the concave side of the tip of the tooth (illustrated in Figs. 2, 4, 6, and 13). The combination of wider-than-expected GLGs and enhanced accessory layers resulted in errors of misinterpreting layers. When the age estimate from these sections was inaccurate, generally age was overestimated. Because of the curvature of the tooth (with the pulp cavity also curving), within a tooth section some of the GLGs appeared on-center while others appeared off-center.

Teeth cut mid-longitudinally yet rotated sagittally relative to the buccal-lingual axis also caused errors, because the resulting GLGs were narrower than with a strictly buccal-lingual cut (because of the non-radially symmetric thinning



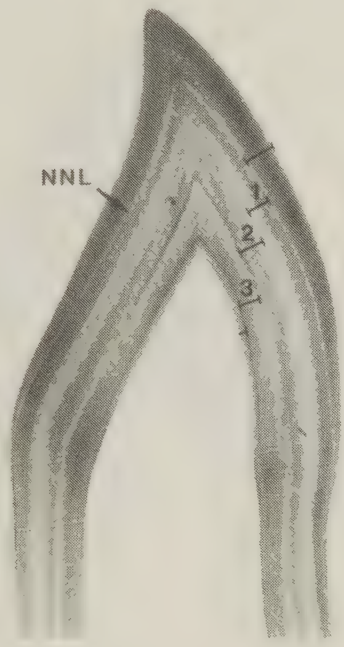
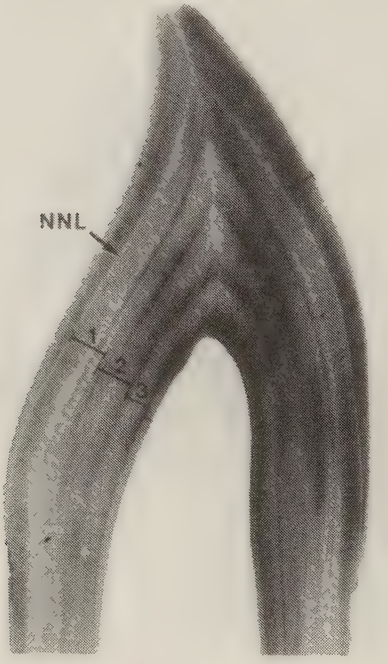


Figure 5. Tooth section from a female (No. 15) known to be 2.2–2.8 yr old. A distinctive accessory layer is apparent in about the center of the first GLG. The GLGs are relatively wide in this tooth, due somewhat to an off-center cut (note that tips of GLGs are blunt rather than sharply pointed). See Figure 2 for explanation of symbols and Table 5 for GLG-thickness measurements.

Figure 6. Tooth section from a known-age 3.0-yr-old female (No. 140). The GLG boundaries are relatively well-defined. There are numerous accessory layers, with some particularly distinct about mid-way through the GLGs. There is a darkly stained narrow layer immediately following the neonatal line. Although this animal was known to be 3.0 yr old at the time the tooth was extracted, there is clearly additional dentinal deposition beyond the apparent end of the third GLG. A new GLG appears to have been forming. See Figure 2 for explanation of symbols and Table 5 for GLG-thickness measurements.

at the tip of the tooth). The narrowing was most evident in the first 2 GLGs, with the other GLGs affected by having their upper portion (near the apices) appear convex. Errors in age estimation appeared to be a result of underestimating due to misinterpreting the end of the relatively narrow first GLG as an accessory layer (*e.g.*, Figs. 12 and 16b).

GLG pattern—The general pattern of GLGs in these bottlenose dolphin teeth is similar to that described in teeth from other dolphins (*e.g.*, from *Stenella* spp., Myrick *et al.* 1983, Perrin and Myrick 1980). Although there is much individual variation, there are characteristics, such as the appearance of boundary and accessory layers and the relative widths of GLGs, that were useful for providing consistency in age estimation. Absence of these guidelines would have produced an incorrect age estimate (*e.g.*, Fig. 7). Conversely, adhering too strictly to the



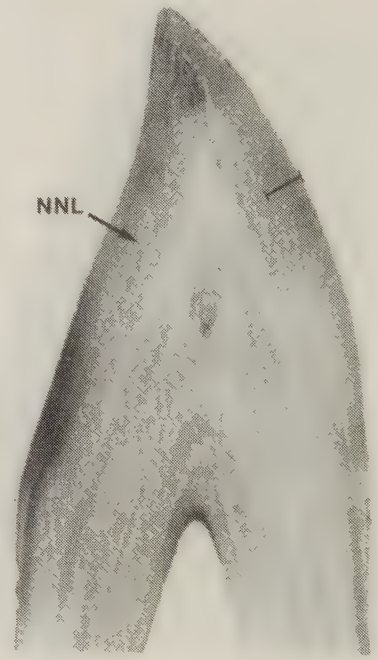
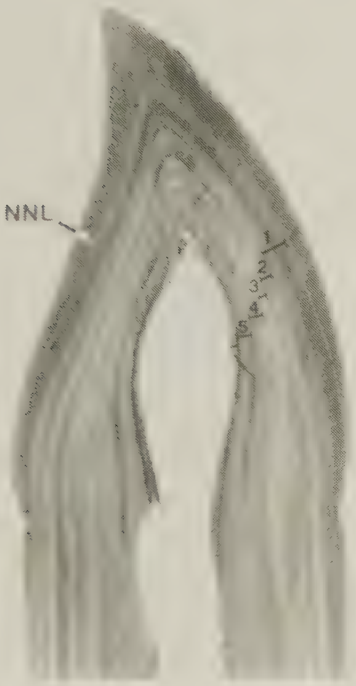


Figure 7. Tooth section from a female (No. 25) known to be greater than 2 but less than 4 yr of age. Two accessory layers, one each in the first and second GLGs, are more conspicuous than the likely boundary between those GLGs. The age from this tooth could easily be estimated to be 4.5 yr. The marked first and second GLGs are provisional. The GLGs have been marked on the opposite side of the tooth to those in the other figures because the layers are clearer there. On the lower, right side of the section, the boundary between GLGs 1 and 2 can be seen as a change in "color" which results from differences in the quantity of stain between the two layers. The layers closer to the pulp cavity are rounded because the section was cut obliquely to the mid-longitudinal axis of the tooth. See Figure 2 for explanation of symbols and Table 5 for GLG-thickness measurements.

Figure 8. Tooth section from a male known to be 3.9–4.0 yr old (No. 67). GLGs are not marked because, as in Figure 4, the correct GLGs were not obvious. The section is a little off-center, possibly contributing to the difficulty in identifying GLGs. Although there are pulp stones (Perrin and Myrick 1980) in the dentine apical to the pulp cavity, they should not necessarily distort the GLG pattern (*e.g.*, see Fig. 10). The boundary between the first and second GLGs is not well-defined. It is very easy to estimate an age of almost 5 GLGs from this section, one year greater than the actual age. See Figure 2 for explanation of symbols.

guidelines produced errors in age estimates because of individual variation (*e.g.*, Fig. 6). The general GLG pattern and specific method used to "read" GLGs and obtain age estimates is given in the Appendix as a guide for estimating age from bottlenose dolphin teeth. A good section (Fig. 2), both in quality of preparation and representative appearance of tooth structures, illustrates the pattern described in the Appendix.



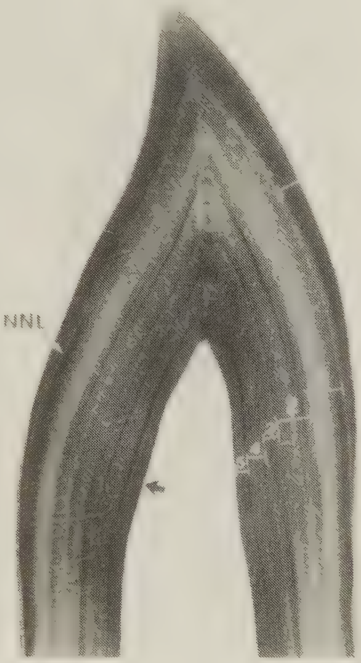
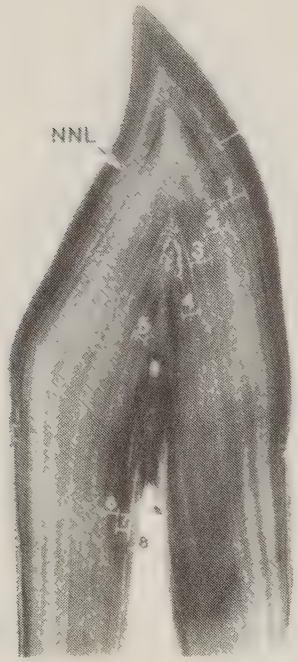


Figure 9. Tooth section from a known-age 5.0-yr-old female (No. 20). This tooth was unusual in that the upper part of the pulp cavity was bulbous, while the area below that was contracted. The unusual appearance reflects how the tooth was growing and is not the result of the way the tooth was sectioned (except the gap on the lower left side of the pulp cavity was tissue torn during sectioning). The result of the unusual growth is that the GLGs are compressed in the upper part of the tooth. As in Figure 6, there is clearly additional dentinal deposition beyond the apparent end of the fifth GLG, although this animal was known to be almost exactly 5.0 yr old at the time the tooth was extracted. See Figure 2 for explanation of symbols and Table 5 for GLG-thickness measurements.

Figure 10. Tooth section from a male (No. 149) known to be 5–6 yr old. The first 2 GLGs are difficult to identify because of the apparent accessory layers. The third GLG is relatively narrow, compared both to the second GLG in this tooth and to the third GLG in teeth from other individuals. Although 5 GLGs are marked, it is possible to imagine 3 GLGs where the first 2 are currently marked, if the prominent accessory layer occurring about centrally in GLG 2 is considered to be the end of a GLG rather than an accessory layer. All of the GLGs would then be about the same width. The decision to identify GLGs as they are marked was made on the basis of the: (1) relative widths of GLGs, (2) common occurrence of a distinct accessory layer in GLG 2 in other individuals in this sample (*e.g.*, see Fig. 3), and (3) relative clarity of the boundary layer between the marked first and second GLGs that extends the length of the section while the accessory layer in the second GLG does not. GLG 5 appears to be complete, indicated by the darkly stained line near the edge of the pulp cavity, and the next GLG is beginning, indicated by the narrow lightly stained area beyond the darkly stained line (see arrow). See Figure 2 for explanation of symbols and Table 5 for GLG-thickness measurements.



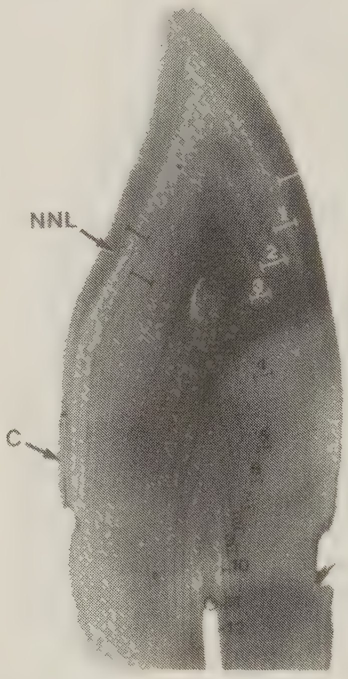


Figure 11. Tooth section from a male (No. 33) known to be 7.7–7.9 yr old. GLGs are countable but difficult to see. Numerous subannual incremental layers can be seen within many of the GLGs. The boundary layers of adjacent GLGs are different from those in many other individuals in that the darkly stained (*i.e.*, relatively hypercalcified) layer is relatively narrow or absent. The prenatal zone, however, has stained similar to that of other individuals, *i.e.*, uniformly and relatively dark compared to much of the postnatal dentine. The unusual appearance of the GLGs apical to the pulp cavity is due to the orientation of the tooth when it was sectioned. See Figure 2 for explanation of symbols and Table 5 for GLG-thickness measurements.

Figure 12. Tooth section from a male (No. 155) known to be 12–14 yr old. The unusual concave appearance at the apex of many of the GLGs results from the tooth being rotated somewhat towards its sagittal axis during sectioning. This rotation facilitates obtaining a section which contains as much of the center of the tooth as possible when the tooth is recurved along its longitudinal axis. As in many strictly mid-longitudinal sections, the boundary layers between GLGs are well-defined and the conspicuous accessory layers about mid-way through the first and second GLGs are visible. Unlike sections cut off-center, the layers are not skewed in such a way as to interfere with the correct identification of GLGs. Possible errors in age estimation may result, however, because the first few GLGs are thinner than they would be if the section were mid-longitudinal. In this section, the accessory layer mid-way through the second GLG could be counted as the end of GLG 1 and the end of GLG 2 could be counted as the end of GLG 3. The result would be an underestimate of age by 1 yr. The last, partial, GLG is barely visible in this photograph. The bar indicating GLG 12 encompasses the last, partial GLG also. GLG 13 is marked, at the circle, at its widest point near the apex of the pulp cavity. A portion of the cementum is indicated (C). See Figure 2 for explanation of other symbols and Table 5 for GLG-thickness measurements.

The thicknesses of temporally corresponding GLGs in longitudinal, on-center sections were similar among individuals of known and approximately known age (where we had the most certainty of identifying the correct GLGs) (Table 5). Differences in orientation of the cut (see above section on sources of error) affected the apparent thickness of layers. An example of differences in measurements can be seen in equivalent GLGs when two teeth were extracted from an individual (Table 6), especially when differences in the orientation of the cut can be observed (Figs. 14–17).

Discussion

This sample of known-age, free-ranging dolphins has provided a unique opportunity to examine the annual layering pattern in teeth and verify methods for estimating age. During that process, we discovered some unexpected results in GLG deposition rates and patterns and were able to investigate the main sources of error in age estimates.

Because for most of the animals age estimates were the same as or close to the known or approximately known age, these results confirm the prior assumption that annual growth layers (= GLGs in this study) occur in the teeth of free-ranging bottlenose dolphins. In addition, most of the GLGs were easily identifiable.

Errors in age estimates were predominantly due to accessory layers which were enhanced by sections that were poorly prepared, suggesting that in many cases it is possible to minimize error by using only well-prepared sections. When sections appear to be poorly prepared, another tooth should be sectioned. For teeth curved in two directions, it can be helpful to prepare two teeth, to minimize distortion of GLGs near the tip of the tooth and near the pulp cavity, especially for old animals. When preparing another tooth is not possible, the degree of deviation of a section from the mid-longitudinal buccal-lingual plane should be considered when counting GLGs. We had only one tooth from most of the animals in our sample so we attempted to estimate age even when the quality of the preparation was poorer than we preferred.

The cause of deposition of GLGs is still unknown. An understanding of this process may help us determine the basis for individual variation in deposition of GLGs and the reason why for three animals we were unable to identify GLGs that corresponded to age. For two of the three (No. 142, Fig. 4 and No. 67, Fig. 8), the correct number of GLGs can be identified if the first layer represents only half a year rather than a full year's growth. All three animals were born in July. Three other animals born in July, however, appear to have a fully formed GLG following the neonatal line. The differences between estimated and known age for these specimens were 0.3, 1.2, and 1.5 yr, the latter two representing some of the greatest differences between known and estimated age.

One interesting and unexpected result was the occurrence of dentine after the end of the last complete GLG in teeth from three animals collected within a month of their date of birth. If GLGs begin at birth and the deposition rate of dentine remains constant throughout the year, these teeth would contain little,

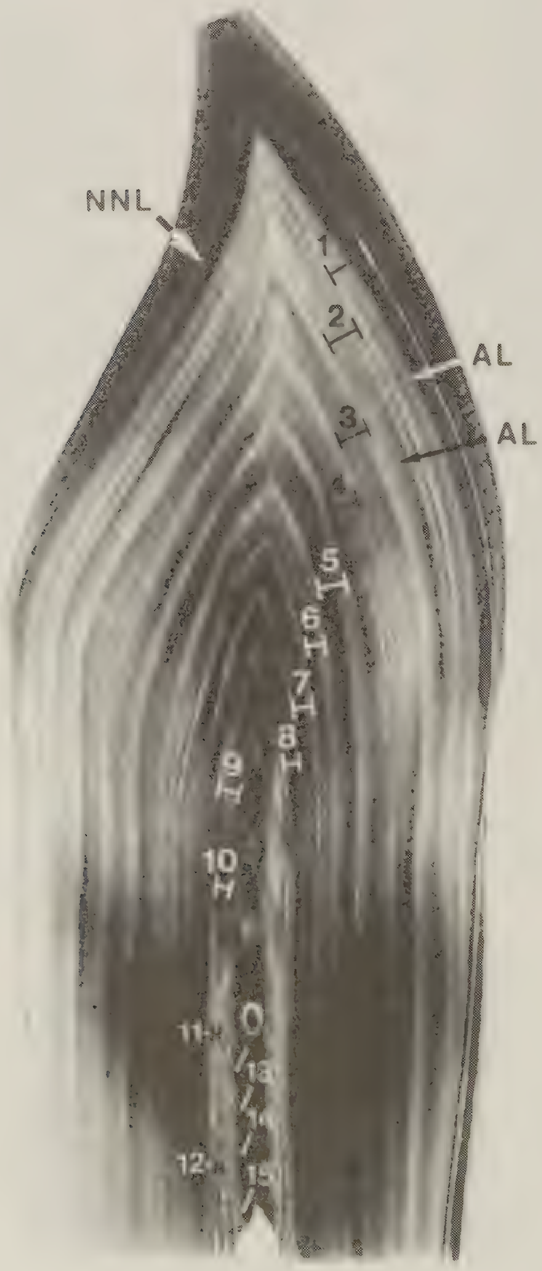


Figure 13. Tooth section from a male (No. 49) known to be 14–16 yr old. Accessory layers (AL) are numerous and those near the center of the first 2 GLGs are particularly distinctive. The appearance of irregular GLGs immediately above the pulp cavity is due to the section being cut sightly off-center near the apex of the pulp cavity. Relying on these GLGs, rather than those on the sides of the pulp cavity where the GLGs are marked,

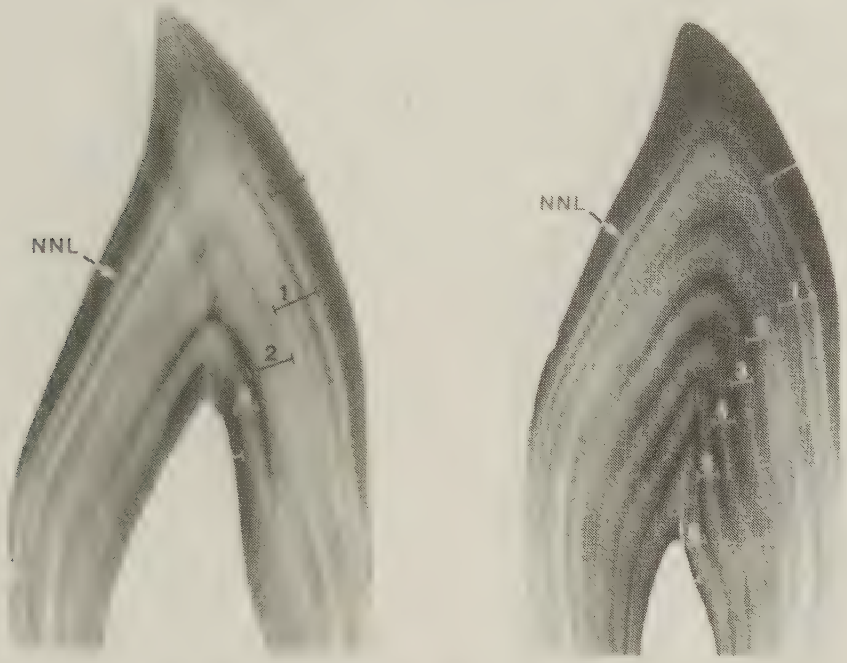


Figure 14. Tooth sections from a known-age female (No. 13) from which two teeth were extracted. The section on the left was extracted in June 1984 when the animal was 3.8 yr old. The section on the right was extracted in January 1987 when the animal was 6.2 yr old. The dashed, vertical line on the second tooth represents the time when the first tooth was extracted. The rounded apices of layers closer to the tip of the tooth and more pointed layers closer to the pulp cavity show that the upper part of the latter section was cut off-center. This orientation skews the GLGs and emphasizes accessory layers in the section of the tooth that is off-center. Aside from artifacts due to preparation differences, the first GLGs in the two teeth are similar in pattern. See Figure 2 for explanation of symbols and Table 6 for GLG-thickness measurements.

if any, dentine forming the next GLG. All of the animals were born in summer, while, on the basis of the relative amount of dentine comprising the new GLG, the last complete GLG appeared to have ended the previous spring. It may be that the onset of layering was triggered by factors other than the calf's birth date. For example, deposition might be influenced in the fetus by the physiology of the mother or an increased light intensity during the spring. Alternatively, new GLGs may begin annually near the date of birth, with dentine deposited at a higher rate in summer than in winter.

←

could result in an overestimated age because accessory layers are visible and easily mistaken for annual layers. See Figure 2 for explanation of other symbols and Table 5 for GLG-thickness measurements.

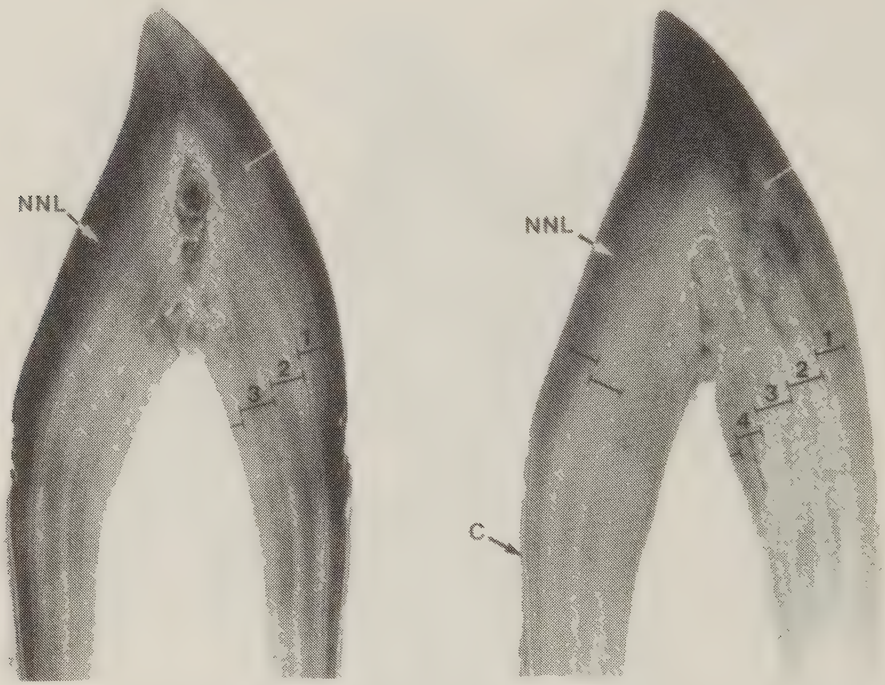


Figure 15. Tooth sections from a female (No. 145) from which two teeth were extracted. The age of the animal is not known. The section on the left is from a tooth extracted in June 1985. The section on the right is from a tooth extracted in June 1986. If the GLGs have been marked correctly, the GLG pattern is atypical in that GLGs 2 and 3 are wider than GLG 1. The pattern may have been distorted by the irregular osteodentine inclusions deposited apical to the pulp cavity. Note that even with the distortion the GLG patterns are identical between the teeth. The dashed, vertical line on the second tooth represents the time when the first tooth was extracted. See Figure 2 for explanation of other symbols and Table 6 for GLG-thickness measurements.

Guide to Age Estimation

The combination of two factors, GLG width and GLG structure, can be used to produce a descriptive "model" for identifying GLGs. Measurements of GLG widths or deposition rates of GLGs have been described for several species (*Tursiops*: Sergeant 1959, Hohn 1980; *Phocoena phocoena*: Nielsen 1972, Gaskin and Blair 1977, van Utrecht 1981; *Lagenorhynchus obscurus*: Best 1976; *Stenella longirostris*: Perrin *et al.* 1977, Myrick *et al.* 1984; *Pontoporia blainvillei*: Kasuya and Brownell 1979; *Globicephala macrorhynchus*: Kasuya and Matsui 1984). These studies include two known-age bottlenose dolphins (Sergeant 1959) and one known-age spinner dolphin (Myrick *et al.* 1984).

The measurements obtained from the bottlenose dolphins described here are virtually the same as those obtained by Sergeant (1959) for the two known-age (0.5 and 2.4 yr) bottlenose dolphins from Florida which were born in

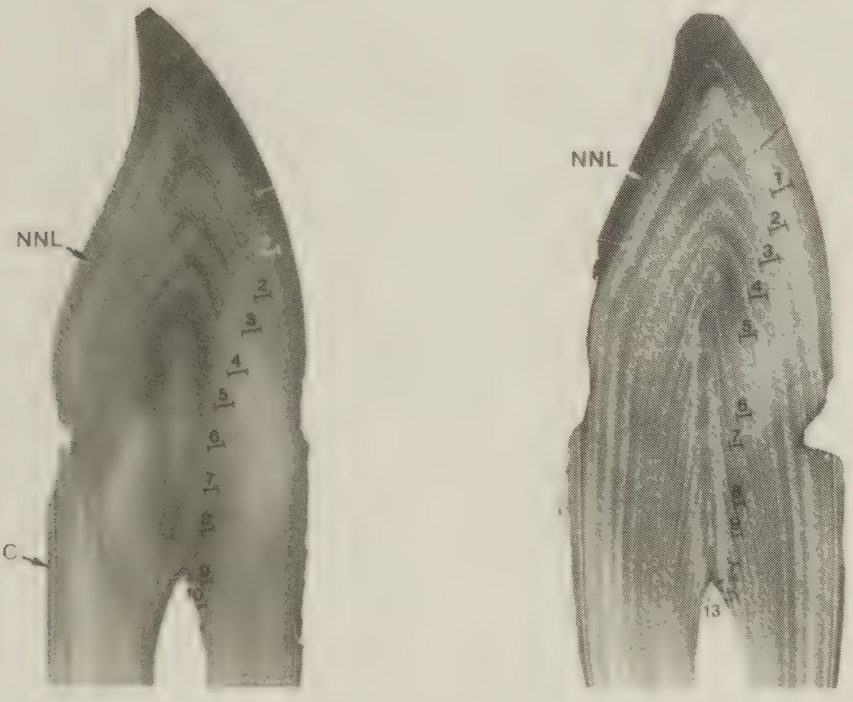


Figure 16. Tooth sections from an approximately known-age male (No. 11). The section on the left was extracted in June 1984 when the animal was 10–11 yr old. The section on the right was extracted in June 1987. As in Figure 10, the tooth was rotated towards it sagittal axis before sectioning, with the same possible errors in age estimation resulting. Accessory layers are particulary visible in the second tooth because the section was better prepared (the tonal unevenness in the first section is from uneven staining). The dashed, vertical line on the second tooth represents the time when the first tooth was extracted. See Figure 2 for explanation of symbols and Table 6 for GLG-thickness measurements.

captivity. It appears, then, that captivity did not alter the GLG pattern for those animals. The measurements given by Hohn (1980) for bottlenose dolphins stranded along the Atlantic coast are lower than those described here because the preparation techniques were different. In the latter study, the sections had not been decalcified. Mounting decalcified and stained sections in glycerin causes some expansion of the tissue, making the GLGs wider relative to sections which have not been so treated. Conversely, dehydrating decalcified sections in alcohol and mounting them in a water-insoluble permanent mounting medium may cause the sections to contract. It is important that the preparation technique be the same if measurements taken from one study are used as a guide in another study.

Variation in widths of corresponding GLGs can also be caused by individual variation, the orientation of the tooth when it was sectioned, and where along

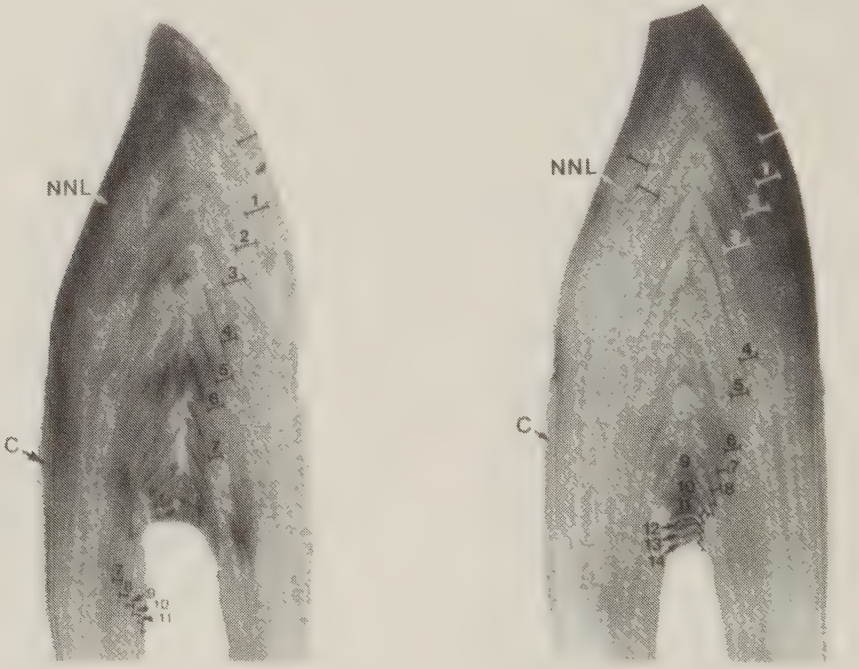


Figure 17. Tooth sections from a male of unknown age (No. 156). The teeth were extracted in June 1984 and June 1987. The dashed line on the second tooth in GLG 12 represents the time when the first tooth was extracted. Marked GLGs 8–11 on the first tooth show where GLG-thickness measurements were taken. Marked GLGs 8–14 on the second tooth show where it is easier to count the GLGs. The flattened appearance of GLGs above the top of the pulp cavity is probably from an off-center cut through a recurved pulp cavity. See Figure 2 for explanation of symbols and Table 6 for GLG-thickness measurements.

the GLG the measurement is taken. These factors speak against the use of absolute measurements to estimate age directly, even for animals taken from the same population, such as done by Myrick *et al.* (1984). Approximate measurements and relative sizes of adjacent GLGs used as a guide for age estimation, however, may decrease the likelihood that accessory layers are interpreted as GLG-boundary layers and increase the likelihood that indistinct boundary layers are not missed.

The measurements given here should be considered approximate because the boundaries of GLGs can only be estimated. The exact boundaries can be known only by application of tetracycline or another marker (or annual extractions) applied on an animal's birthday each year.

In addition to using measurements as a guide for identifying GLGs, knowledge of any subannual layering pattern is important. The annual layering pattern in teeth and bones has often been described as a "double layer" pattern (Klevezal' 1980), as the deposition of two layers per year (Goren *et al.* 1987), or as a

Table 4. Age estimates for free-ranging bottlenose dolphins from which a second tooth was extracted after a known time-interval following the first extraction. The second tooth from specimens 154 and 11 was taken after the animals were found beach-cast. Specimen 13 was of known age, 3 and 11 of approximately known age, and 154 and 156 of minimum known age, while 145 had no prior age data available.

	ID no.					
	13	145	154	3	11	156
Figure no.	14	15			16	17
Date of birth (mo/yr)	9/80	—	—	212-cm calf in 1976	190-cm calf in 1976	—
First tooth extraction:						
Date (mo/d/yr)	6/28/84	6/25/85	6/22/84	6/22/84	6/22/84	6/21/84
Body length (cm)	219	218	245	253	256	261
Estimated age (yr)	—[a]	3.7	3.4	10.5	9.5[b]	11.5[b]
Probable age[c] (yr)	3.8	3.6	4.4	10.5	10.5	11.5
Second tooth extraction:						
Time between extractions	2.5 yr	1 yr	0.4 yr	3 yr	3.1 yr	3 yr
Date (mo/d/yr)	1/06/87	6/24/86	11/05/84	6/22/87	7/31/87	6/26/87
Body length (cm)	233	220	252	265	261	263
Estimated age (yr)	6.2[b]	4.8	4.8[b]	14.5	—[b,d]	14.1
Probable age[c] (yr)	6.2	4.6	4.8	13.5	13.5	14.5

[a] The first tooth collected from animal No. 13 was used to examine the growth layer pattern before the other teeth were read. The second tooth collected from this animal was read in the blind.

[b] Quality of preparation of the tooth sections poor.

[c] Probable age was determined by examining the GLGs in both teeth with knowledge of the time between extractions after the original estimates had been made.

[d] The second tooth from this animal was received after the other teeth had been completed. Age was not estimated.

Table 5. Thickness (μm) of the prenatal zone (PZ) and GLGs measured from teeth of known-age and approximately known-age free-ranging bottlenose dolphins from which a single tooth was extracted. The last measurement for each specimen represents a partial GLG and is not included in the mean. The location on the tooth sections where the measurements were taken are shown in the figures for these specimens.

ID no.	Age (yr)	PZ	GLG number 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Sections cut mid-longitudinally ("good" preparations):																	
148	2.3	705	578	451	222												
147	2.5	768	787	672	221												
157	2.6	816	835	826	307												
61	3.0	763	941	749	691	125											
140	3.0	710	566	509	499	173											
25	3.4	746	852	852	488	144											
12	3.4	785	842	785	699	239											
149	5.1	642	790	692	383	371	321	12									
33	7.8	642	725	696	598[a]												
49	15.5	739	701	552	538	528	461	346	302	226	158	139	144	115[a]			
Mean:		732	762	678	557												
SE:		18	38	43	43												
Sections cut obliquely relative to the longitudinal axis (off-center):																	
15	2.4	775	976	861	335												
17	3.8	787	1,018	1,046	595	317											
06	5.8	660	797	739	586	432	384	240									
Sections cut with the tooth rotated towards the sagittal axis:																	
155	12.3	656	643	605	451	418	336	264	326	240	202	182	134	82	19		
14	14.5	682	576	509	461	422	384	374	355	346	230	163	106	86	72	58	29

[a] Due to the orientation of the cut through the pulp cavity, remaining GLG measurements would not be comparable to the previous measurements.

Table 6. Thickness (μm) of the prenatal zone (PZ) and the GLGs in teeth from free-ranging bottlenose dolphins from which two teeth were extracted. The last measurement on each tooth represents a partial GLG. The locations where the measurements were taken on tooth sections are shown in the figures for these specimens.

	Age		GLG number														
ID no.	(yr)	PZ	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
13	3.8	775	890	880	490	211											
13	6.2	749	835	811	494	490	480	432	91								
145	3.8	835	682	787	806	240											
145	4.8	730	662	701	816	518	221										
154	4.4	787	605	557	595	490	168										
154	4.8	758	595	634	614	509	432										
3[a]	10.5	672	1,094	778	634	451	451	403	384	365	307	221	67				
3[a]	13.5	528	979	768	509	422	298	259	240	173	158	134	125	96	96	38	
11	10.5	701	624	480	576	528	605	442	413	384	307	202	77				
11	13.5	677	566	538	576	451	432	394	355	278	264	250	163	144	115	48	
156	11.5	653	730	691	595	576	538	355	259	240	192	182	163	58			
156	14.5	691	739	730	691	538	509	442	336	269	125	96	163	163	134	144	48

[a] Sections cut off-center.

single layer with a distinct mid-GLG accessory layer (Hohn 1980). The different descriptions illustrate that annual layers consist of a pattern which often includes a distinctive dark-staining layer near the center (see Klevezal' 1980). Although these layers may contain some intrinsic information of value (*e.g.,* weaning marks), they can be considered as "noise" for the purpose of identifying GLGs (see Hohn, in press). When incorrect age estimates are made in a consistent, biased manner for a sample of dolphins, it is probably due to the reader mistaking an accessory layer for a GLG-boundary layer. This error seems to be most prevalent in the first two GLGs (Hohn, in press). In young animals, the age estimate would be about twice the age, whereas for older animals the age estimate will be high by about two years (see Hohn, in press). Any guide or "model" for estimating age from dolphin teeth must take into account that accessory layers are often a part of the GLG pattern.

Conclusion

Annual layers are clearly present in these teeth from known-age, free-ranging bottlenose dolphins. We suggest that when age is incorrectly estimated, it is due to incorrect identification of annual growth layers, rather than a lack of them. In addition, given a correct model of GLG patterns, the precision of age estimates will increase with increasing quality of preparation of sections.

We do not know to what extent these results can be applied directly to other species of dolphins, but the GLG patterns and relative size of the GLGs are very similar in many delphinids (see Perrin and Myrick 1980, Hohn, in press). We suggest that the GLG pattern and relative GLG thickness (but not absolute thickness) described in these teeth from known-age, free-ranging bottlenose dolphins be used as a model of GLG deposition and applied to other delphinid species for which the layers have not been calibrated. This would allow for some standardization of methodology for dolphin age estimation.

Acknowledgments

S. Chivers, C. Dargan, and S. Kruse helped with preparation of the tooth sections. H. Orr photographed the tooth sections and labeled the figures. Teeth from beach-cast specimens were provided by J. Patton, Mote Marine Laboratory (MML). Fieldwork during 1970–1971 was supported by MML and the Office of Naval Research, during 1975–1976 by the U.S. Marine Mammal Commission, during 1980 by the Southeast Fisheries Center, during 1980–1981 by the University of California at Santa Cruz, and from 1982 to the present by the Center for Field Research/Earthwatch, the Inter-American Tropical Tuna Commission, and by contributions of funds, equipment, and time to Dolphin Biology Research Associates, Inc. The Sirenia Research Group of the U.S. Fish and Wildlife Service and F. and J. Wells provided essential equipment and logistical support. L. Fulford made possible the safe and successful capture of dolphins from 1984 to the present. D. DeMaster, D. Gaskin, C. Lockyer, and W. Perrin reviewed the manuscript.

Literature Cited

Best, P. B. 1976. Tetracycline marking and the rate of growth layer formation in the teeth of a dolphin. South African Journal of Science 72:216–218.

Gaskin, D. E., and B. A. Blair. 1977. Age determination of harbour porpoise, *Phocoena phocoena* (L.), in the western North Atlantic. Canadian Journal of Zoology 55: 18–30.

Goren, A. D., P. F. Brodie, S. Spotte, G. C. Ray, H. W. Kaufman, A. J. Gwinnett, J. J. Sciubba and J. D. Buck. 1987. Growth layer groups (GLGs) in the teeth of an adult belukha whale (*Delphinapterus leucas*) of known age: evidence for two annual layers. Marine Mammal Science 3:14–21.

Grue, H., and B. Jensen. 1979. Review of the formation of incremental lines in tooth cementum of terrestrial mammals. Danish Review of Game Biology 11:1–48.

Harrison, R. J., R. L. Brownell, Jr. and R. C. Boice. 1972. Reproduction and gonadal appearances in some odontocetes. Pages 362–429 *in* R. J. Harrison, ed. Functional anatomy of marine mammals. Vol. 1. Academic Press, New York.

Hohn, A. A. 1980. Age determination and age-related factors in the teeth of western North Atlantic bottlenose dolphins. Scientific Reports of the Whales Research Institute, Tokyo 32:39–66.

Hohn, A. A. in press. Reading between the lines: an analysis of age estimation in dolphins. *In* S. Leatherwood and R. R. Reeves, eds. The bottlenose dolphin. Academic Press, New York.

Hohn, A. A., and P. S. Hammond. 1985. Early postnatal growth of the spotted dolphins. *Stenella attenuata*, in the offshore eastern tropical Pacific. Fishery Bulletin 83:553–566.

Hui, C. A. 1980. Variability of dentin deposits in *Tursiops truncatus*. Canadian Journal of Fisheries and Aquatic Science 37:712–716.

Irvine, A. B., and R. S. Wells. 1972. Results of attempts to tag Atlantic bottlenosed dolphins, *Tursiops truncatus*. Cetology 13:1–5.

Irvine, A. B., M. D. Scott, R. S. Wells and J. H. Kaufmann. 1981. Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. Fishery Bulletin 79:671–688.

Kasuya, T., and R. L. Brownell, Jr. 1979. Age determination, reproduction, and growth of franciscana dolphin, *Pontoporia blainvillei*. Scientific Reports of the Whales Research Institute, Tokyo 31:45–67.

Kasuya, T., and S. Matsui. 1984. Age determination and growth of the short-finned pilot whale off the Pacific coast of Japan. Scientific Reports of the Whales Research Institute, Tokyo 35:57–91.

Klevezal', G. A. 1980. Layers in the hard tissues of mammals as a record of growth rhythms of individuals. Reports of the International Whaling Commission (Special Issue 3):161–164.

Klevezal', G. A., and S. E. Kleinenberg. 1967. Opredelenie vozrasta mlekopitayushchikh po sloistym strukturam zubov i kosti. Izdatel'stvo "Nauka," Moscow, 144 pp. [Translation] 1969. Age determination of mammals from annual layers in teeth and bone. Israeli Program for Scientific Translation, Jerusalem, 128 pp.

Myrick, A. C., Jr., A. A. Hohn, P. A. Sloan, M. Kimura and D. D. Stanley. 1983. Estimating age of spotted and spinner dolphins (*Stenella attenuata* and *Stenella longirostris*) from teeth. National Oceanic and Atmospheric Administration Technical Report NMFS 30. 17 pp.

Myrick, A. C., Jr., E. W. Shallenberger, I. Kang and D. B. Mackay. 1984. Calibration of dental layers in seven captive Hawaiian spinner dolphins, *Stenella longirostris*, based on tetracycline labeling. Fishery Bulletin 82:207–225.

Nielsen, H. G. 1972. Age determination of the harbour porpoise *Phocoena phocoena* (L.) (Cetacea). Videnskabelige Meddelelser fra dansk Naturhistoric Forening 135: 61–84.

Perrin, W. F., D. B. Holts and R. B. Miller. 1977. Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenella longirostris* in the eastern tropical Pacific. Fishery Bulletin 75:725–750.

Perrin, W. F., and A. C. Myrick, Jr., eds. 1980. Age determination of toothed whales and sirenians. Reports of the International Whaling Commission (Special Issue 3), Cambridge. 229 pp.

RIDGWAY, S. H., R. F. GREEN AND J. C. SWEENEY. 1975. Mandibular anesthesia and tooth extraction in the bottlenosed dolphin. Journal of Wildlife Diseases 11:415–418.

SERGEANT, D. E. 1959. Age determination in odontocete whales from dentinal growth layers. Norweigian Whaling Gazette 6:273–288.

SERGEANT, D. E., D. K. CALDWELL AND M. C. CALDWELL. 1973. Age, growth, and maturity of bottlenosed dolphin (*Tursiops truncatus*) from northeast Florida. Journal of the Fisheries Research Board of Canada 30:1009–1011.

UTRECHT, W. L. VAN. 1981. Comparison of accumulation patterns in layered dentinal tissue of some Odontoceti and corresponding patterns in baleen plates and ear plugs of Balaenopteridae. Beaufortia 31:111–122.

WELLS, R. S. 1986. Structural aspects of dolphin societies. Ph.D. dissertation. University of California, Santa Cruz. 234 pp.

WELLS, R. S., A. B. IRVINE AND M. D. SCOTT. 1980. The social ecology of inshore odontocetes. Pages 263–318 *in* L. M. Herman, ed. Cetacean behavior: mechanisms and functions. Wiley-Interscience Press, New York.

WELLS, R. S., M. D. SCOTT AND A. B. IRVINE. 1987. The social structure of free-ranging bottlenose dolphins. Pages 247–305 *in* H. Genoways, ed. Current mammalogy. Vol. 1. Plenum Publishing Corp., New York.

Received: February 22, 1988
Accepted: June 8, 1989

APPENDIX 1

READER'S GUIDE TO DOLPHIN TEETH

Documentation of the procedure used to estimate the age of known-age dolphins. Provided is a step-by-step guide to estimating age from mid-longitudinal sections of dolphin teeth which have been decalcified and stained. The user is required to have some basic knowledge of the structures found in dolphin teeth and terminology for those structures, a primer for which can be found in Perrin and Myrick (1980). See Figure 2 as a guide for the structures discussed.

Step-By-Step-Procedure	Explanation
1. Examine the entire section, tip to base and on both sides of the pulp cavity, for the general GLG pattern for that specimen. 2. Find the buccal (convex) side of the section and the neonatal line. 3. Identify a point about one-third the distance from the tip of the tooth to the base of the prenatal zone. (The base of the prenatal zone is where the neonatal line converges with the outside edge of the tooth.) 4. Measure or approximate the thickness of the prenatal zone (perpendicular from the outside edge of tooth to the neonatal line) at this point. 5. Find an area in the postnatal dentine above the base of the prenatal zone where the thickness of the layers is relatively constant. 6. Use the previously determioned prenatal zone thickness as a guide to find the end of the first GLG.	A. Getting started: Where is the first annual growth layer? (We will equate annual growth layer with a growth layer group, GLG, for this sample). This GLG is the most difficult and important to identify correctly. It is the most difficult because often (a) the boundary layer between the first and second GLGs is not distinct, and (b) there may be accessory layers near the centers of the first and second GLGs that are more distinct than the boundary layer between those GLGs. It is the most important because the subsequent GLGs are found relative to it. It is helpful to start the process of age estimation by examining the entire section to become familiar with the GLG pattern for that specimen. A guideline for finding the first GLG is that the thickness of this layer is approximately the same thickness as the prenatal zone at a point in the prenatal zone about one-third the distance from the tip of the tooth to the base of the prenatal zone on the buccal (convex) side of the tooth. The first GLG is then determined in the upper part of the tooth in an area where the width does not change over a short distance, *e.g.*, about half-way from the tip of the tooth to the base of the prenatal zone. The area chosen for these approximations is important since the prenatal zone is widest at the tip and narrows quickly as it approaches its base. In addition, in sections cut off-center or obliquely, the GLGs appear wider or narrower close to the tip of the tooth.
7. Look for the end of the first GLG as a thin, stained layer which may be readily visible only near the tip of the section or as an abrupt change in dentinal color.	B. Finding the end of the first GLG: Ideally, and often, the boundary layers of the GLGs appear as darkly stained narrow layers. In the first GLG, this layer can be difficult to locate and it may appear almost undifferentiated from the surrounding dentine. Sometimes the boundary layer for the first GLG is readily apparent only in the upper part of the tooth section as a fine line or in the root of the tooth as an abrubt change in color resulting from

APPENDIX 1

Continued.

Step-By-Step-Procedure	Explanation
	different stainability of the dentine in the first and second GLGs. Be careful to not confuse an accessory layer with the boundary layer.
8. For the second and subsequent GLGs, the relative measurements are made closer and closer to the root of the tooth as one counts inwards towards the pulp cavity. 9. To find the second GLG, repeat the procedure described above, beginning at the end of the first GLG. Make the same perpendicular measurement from the beginning of the second GLG. Look for the end of the second GLG as a well stained, relatively distinct layer.	C. The second GLG is about the same width as the first GLG. In at least bottlenose (*Tursiops truncatus*) and spotted dolphins (*Stenella attenuata*), the end of the second GLG, or the boundary layer between the second and third, is a very distinct, darkly stained layer generally more distinctive than the boundary layer between the first and second GLGs. In specimens older than a few years, it is generally easier to find this boundary layer than the one between the first two GLGs. The relative measurement is made slightly closer to the root of the tooth than the previous one (*e.g.,* see Fig. 2).
10. To find the third GLG, again repeat the above procedure, but expect the third GLG to be thinner than the second.	D. The third GLG is thinner than the second GLG. It is, on average, 77% of the thickness of the second GLG in good preparations in the known-age sample. In bottlenose and spotted dolphins, the end of the third GLG is distinct, but not as distinct as that of the second GLG.
11. Repeat the procedure for the fourth GLG. It will be about the same thickness as the third GLG.	E. The fourth GLG is about the same thickness as or somewhat thinner than the third. In bottlenose and spotted dolphins, its boundary layer is very distinct, often even more so than that of the second GLG.
12. Look for subsequent GLGs to be about the same thickness or somewhat thinner than the previous GLG.	F. After GLG four: The layers become progressively narrower, although adjacent GLGs will be about the same thickness. Unless dentinal growth becomes distorted or "irregular," subsequent layers generally are not thicker than previous layers.
13. Look again at the pattern of GLG deposition for each specimen being examined and follow that pattern to count the remaining GLGs.	

8928

SC/40/SM12

Monitoring Trends in Dolphin Abundance in the Eastern Tropical Pacific using Research Vessels over a Long Sampling Period: Analyses of 1987 Data

Rennie S. Holt and Stephanie N. Sexton

National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA, USA

ABSTRACT

During 1987, the National Marine Fisheries Service conducted the second in its series of long-term research ship surveys to determine status of dolphin stocks taken incidentally by tuna purse seiners in the eastern tropical Pacific. Line transect methodology was used by observers aboard two vessels for 120 days each. Relative abundance estimates of northern offshore spotted dolphins are approximately 1,300,000 animals with a coefficient of variation of 0.262. This estimate was larger than the 1986 estimate of 929,000 northern offshore spotted dolphins. Relative sizes of other stocks also varied. We examine reasons for these differences and discuss alternative methods of stratifying the data.

INTRODUCTION

The National Marine Fisheries Service (NMFS) is responsible for assessing the status of those dolphin stocks taken incidentally by tuna purse seiners in the eastern tropical Pacific (ETP) (Richey, 1976). The status of the spotted dolphin, *Stenella attenuata*, is of special concern because it is the major species taken by the fishery (Smith, 1979). Of the spotted dolphins, the northern offshore stock is considered to be the most affected by the fishery because it has been fished more frequently than any other stock. The spinner dolphin, *S. longirostris*, and the common dolphin, *Delphinus delphis*, are also taken. The striped dolphin, *S. coeruleoalba*, and Fraser's dolphin, *Lagenodelphis hosei*, are occasionally caught but are difficult to distinguish from the other three species at a distance (Holt and Powers, 1982). These five species are herein grouped and termed target species.

In 1986, the NMFS initiated a research program to monitor relative abundance of dolphin populations in the ETP using two research vessels for at least five years during which six surveys will be conducted. The research design for the surveys, presented by Holt, Gerrodette and Cologne (1987), indicated that a 10% annual rate of decrease in northern offshore spotted dolphins could be detected (a total 41% decrease over six surveys) with alpha and beta error levels of 10%. Analyses of the 1986 data are presented by Holt and Sexton (1988a). In 1987, the NMFS conducted a second survey using the same vessels at the same time of the year. Herein, we present relative abundance estimates for the 1987 data and compare these to the 1986 estimates. We also discuss effects of several alternate stratification methods and data treatment factors on these estimates. Because we desire to determine change in population size over several years and not estimate absolute abundance, data from several years will eventually be used to select the most consistent relative indicator of population change.

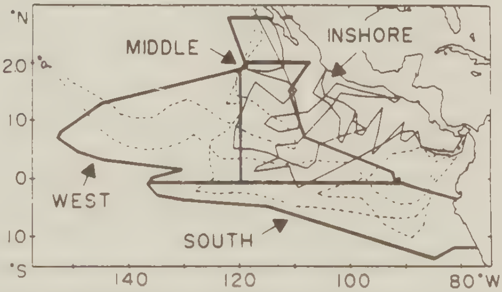


Fig. 1. Tracklines traversed by the NOAA R/V *David Starr Jordan* (solid) and *McArthur* (dash) during the 1987 survey. Tracklines generated using noontime positions.

MATERIALS AND METHODS

Study area and survey coverage

The study area and area strata were those used during the 1986 survey (Holt and Sexton, 1988a). The research vessels *McArthur* and *David Starr Jordan* traversed predetermined tracklines in the ETP from 30 July and 8 August, respectively, through 10 December (Fig. 1). Each ship was scheduled to spend approximately 120 days at sea but the *Jordan* departed 10 days late. Ship itineries, list of scientific personnel, survey equipment, data collection procedures and preliminary data summaries for each ship are presented by Holt and Sexton (1988b) and Holt and Jackson (1988). Only those factors important to this paper are presented here.

On each ship, two observers used 25X binoculars located on each side of the ship to search from directly ahead to abeam of their respective sides of the ship. A third observer served as data recorder and searched directly ahead of the ship when not recording data. Two teams of three observers each alternatively occupied the three duty stations. Each team was on duty for 2-hour shifts. During each shift, members spent approximately equal time occupying each duty station. Two of the six observers had completed several marine mammal cruises in the ETP and were experts in identifying marine mammals. These two identification specialists were assigned to separate teams such that one would always be on duty. Teams members did not change during the cruises. Observers switched ships at the mid-point of the cruises.

When possible, schools were approached and observers recorded independent 'best' estimates of school size. In some cases, an observer obtained a 'minimum' estimate but could not provide a best estimate. Independent estimates were averaged to obtain mean minimum and best estimates. When weather conditions were suitable, a *Hughes* 500D helicopter, based aboard the *Jordan* was used to photograph schools whose sizes were estimated by the observers. The photographs will be used to calibrate observer estimates of school sizes.

Abundance estimation

Relative estimates of population abundance of the target species (N_{ij}) were computed as (Holt and Sexton, 1988a):

$$N_{ij} = \sum_{k=1}^{4} (D_k S_{tk} P_{tk} P_{ik} A_k / A_{ik})(A_{ijk} + P'_{ij} A'_{ijk}), \quad (1)$$

where

D_k = estimate of density of schools of all dolphin species in area k,

S_{tk} = estimate of mean size of schools of all target species in area k,

P_{tk} = estimate of proportion of all dolphin schools which are target schools in area k,

P_{ik} = estimate of proportion of individuals of species i in target schools in area k,

P'_{ij} = estimate of proportion of individuals of stock j of species i in target schools in overlap region containing two stocks of species i (overlap region discussed in text),

A_k = total area inhabited by all target species in area k,

A_{ik} = area inhabited by species i in area k,

A_{ijk} = area inhabited by species i, stock j, in area k, and

A'_{ijk} = area inhabited by species i, stock j, in overlap region of area k.

The variance of N_{ij} was calculated using bootstrap methods. For each stratum, the number of legs of searching effort was tabulated and then effort legs equal to that number were randomly selected with replacement. This effort and the associated sightings were used to calculate school density, school size, species proportions and finally estimates of N_{ij}s. This was repeated 100 times. The variance of N_{ij} for each stock was calculated using these 100 estimates.

Formulae used to estimate school density are from Burnham, Anderson and Laake (1980), Holt (1985, 1987), and Hayes and Buckland (1983). The Fourier series (Cain *et al.*, 1979) and hazard rate (Hayes and Buckland, 1983; Buckland, 1985) models both provided adequate fits (similar point estimates and chi-square values) to the data but the hazard rate model was used because, unlike the Fourier series model, its use does not require subjective selection of the number of terms in the model and, therefore, could be used in the bootstrap procedures. Of schools containing both target and non-target species, only the proportion of individuals of the target species was used in the school size estimate. Estimates of the proportion of all dolphin schools that were target schools (P_{tk}) were calculated using formulae presented by Holt and Powers (1982). Formulae to estimate the proportions (P_{ik}) of the number of individuals for each species of all target individuals are given by Barlow and Holt (1986).

All species of dolphins encountered in the study area were included in the density analyses. Estimates were calculated using only schools containing 15 or more animals. Smaller schools were not used because we believe small schools both on and off the ships' tracklines may be difficult to detect especially during rough weather and may have been missed at a variable rate depending upon prevailing weather conditions (Holt, 1987).

Only schools detected within 3.7km (2.0 n.miles) perpendicular distance of the trackline were used to estimate school density because a 3.7-km truncation point provided the best fit of the model to this data. It was chosen because the perpendicular distance distributions of schools detected at greater distances were 'spiked' and because schools detected at greater than 3.7km have little effect on the density estimates. Schools detected at increasing distances from the trackline tend to include disproportionately more large schools because there is a direct correlation between the size of a school and the probability of it being detected (Drummer, 1985). This biases school size estimates upwards and species proportions toward species which occur in large schools. We attempted to adjust for this bias by weighting school size and species proportion estimates by the inverse of logarithm of school size (Holt and Powers, 1982). Finally, schools for which there were no 'best' estimates were not used in the school size or species proportion calculations.

Some stocks of the same species overlap geographic areas (A'_{ijk}). These overlapping stocks include (1) coastal and northern spotted, (2) eastern and whitebelly spinner and (3) Baja Neritic and northern common dolphins (Perrin *et al.*, 1984). The relative number of dolphins of each overlapping stock (P'_{ij}) was calculated for data pooled over strata. Because of small sample sizes, the pooled estimate of P'_{ij} was used in each of the bootstrapped iterations. For overlapping stocks of spotted dolphins and for spinner dolphins, the relative proportions of coastal and northern spotted and of eastern and whitebelly spinner stocks within their area of overlap were calculated as the averages of their relative abundances (percent occurrence). Few data were available to determine relative proportions of the overlapping Baja Neritic and northern common dolphins. Therefore, population estimates for Baja Neritic were combined with northern common dolphins.

The area inhabited by each target species (A_k) used to calculate the population abundance estimates were those defined by Au *et al.* (1979) and Perrin *et al.* (1984). The study area was partitioned into four strata (Holt and Sexton, 1988a). All four strata comprise the total area. The size of each stratum and the area occupied by each stock in each stratum was calculated by Holt and Sexton (1988a).

RESULTS

During the entire survey, observers aboard both vessels searched 28,611km and detected 1,249 marine mammal schools. Dolphins were present in 891 of these schools. While searching in the study area (Fig. 1), within 3.7km perpendicular distance of the trackline, and during Beaufort Sea states of 5 or less, observers on both vessels searched 26,519km and detected 352 dolphin schools (Table 1). The amount of effort and schools detected varied among strata; 42% of the total trackline searched and 53% of all schools detected were in the inshore area.

Table 1

1987 cruise data and results (see text) Data were truncated at 3.7km perpendicular distance. Schools with less than 15 animals were omitted from analyses. School sizes and species proportions were weighted by inverse of school size. Effort collecting during sea states 0 – 5 included in analyses. Data summed for both vessels. Total is for data summed over all four strata

	Inshore	Middle	West	South	Total
Area (1,000km^2)	5,693	3,798	5,298	4,359	19,148
% Total area	30	20	28	22	100
Trackline searched (km)	11,145	7,974	3,529	3,871	26,519
% searching effort	42	30	13	15	100
Density ($\hat{D}_k$)[1]	4.74	3.15	2.16	3.58	3.75
No. schools detected[a]	187	89	27	49	352
Mean target species school size (S_{tk})	81.57	84.56	94.12	121.64	88.39
No. target schools[b]	151	77	23	38	289
Proportions:					
Target schools (P_{tk})	0.826	0.858	0.802	0.865	0.837
Spotted dolphins	0.284	0.524	0.367	0.319	0.360
Spinner dolphins	0.201	0.258	0.315	0.167	0.219
Common dolphins	0.272	0.009	0.056	0.080	0.152
Striped dolphins	0.242	0.159	0.046	0.295	0.214
Fraser's dolphins	0.000	0.050	0.217	0.139	0.055
Overlap area:					
Prop. Coastal Spotted					0.182
Prop. Offshore Spotted					0.818
No. Spotted schools					18
Prop. Eastern Spinner					0.677
Prop. Whitebelly Spinner					0.323
No. Spinner schools					83

[1] schools/1.000 km^2

[a] including unidentified dolphin schools.

[b] including schools identified as target species but for which a best estimate of school size was not made

The estimate of f(0) for data in the total area was 0.577. Density estimates (D_k) in the four strata, calculated using the pooled f(0), ranged from 2.21 to 4.84 schools/1000km^2 (Table 1). Estimates of mean school size (S_{tk}) of target species ranged from 81.57 to 121.64 animals (Table 1). The proportion of identified dolphin schools that included target species (P_{tk}) ranged from 0.826 to 0.900 among strata (Table 1).

The proportions of individuals of target species that were spotted dolphins (P_{ik}) ranged from 0.284 to 0.524 among the strata (Table 1). The proportions of the other target species among strata also varied greatly. For example, the proportion of common dolphins ranged from 0.009 to 0.272 (Table 1). Only 18 spotted dolphin schools were detected in the overlap region of the coastal and offshore spotted stocks. The proportion (P'_{ij}) of these that were offshore spotted dolphins was 0.818 (Table 1). Of 83 spinner dolphin schools detected in the area of overlap of eastern and whitebelly spinner stocks, 0.677 were eastern spinner dolphin schools.

The estimate of relative abundance for each stock of the target species is presented in Table 2. Spotted dolphins were the most abundant target species. The estimate of 1,275,400 northern offshore spotted dolphins represented 70% of the estimate of all stocks of spotted dolphins. The coefficient of variation of the abundance of the northern offshore spotted stock, CV(N_{ij}), was 0.262. The abundance estimate for eastern spinner dolphins was 533,100 animals with a CV of 0.281.

DISCUSSION

Table 2

Estimates of population sizes (N_{ij}) (in thousands of animals) by stock for target species in total area Values given are weighted by stratum.

Species/stock	N_{ij}	SE(N_{ij})	CV(N_{ij})
Spotted			
Coastal	32.4	6.8	0.210
Northern Offshore	1,275.4	334.3	0.262
Southern Offshore	501.8	199.8	0.398
Total	1,809.6	540.9	0.299
Spinner			
Costa Rican	17.9	4.6	0.257
Eastern	533.2	149.8	0.281
Northern Whitebelly	334.2	96.9	0.290
Southern Whitebelly	252.2	105.1	0.417
Total	1,137.5	356.4	0.313
[illegible]			
Northern Tropical	130.3	47.7	0.366
West Central Tropical	53.0	44.8	0.845
East Central Tropical	307.0	112.0	0.365
Southern Tropical	201.0	110.7	0.551
Total	691.3	315.2	0.456
Striped			
Northern Tropical	124.4	23.0	0.185
West Central Tropical	33.7	23.8	0.706
East Central Tropical	353.9	63.1	0.178
Southern Tropical	584.2	147.8	0.253
Total	1,096.2	257.7	0.235
Fraser's	451.0	282.5	0.626
Total	5,185.6	1,752.7	0.338

Abundance estimates may be calculated using equation (1) by pooling variables across geographical strata and/or species categories. In general, the greater the degree of pooling across variables, the more precise (lower CVs) but also the more biased are estimates of abundance. For example, we calculated the density estimate (D_k) by pooling perpendicular distance distributions across strata such that

$$D_k = \sum_{k=1}^{n} n_k f(0)/2l_k.$$

where n_k is the number of dolphin schools detected in stratum k and l_k is the line length searched in stratum k.

An alternate method was examined which calculated f(0) for data in each stratum. This yielded an abundance estimate for northern offshore spotted dolphins of 1,576,600 animals compared to our estimate of 1,275,400 animals (Table 2) but the estimate of CV was 0.363 compared to 0.262 for our pooled f(0) method. The larger CV resulted because the hazard rate model was applied to small data sets in the south (27 schools) and west (49 schools) strata (Table 1).

We also investigated another alternate method by calculating abundance estimates for all variables in equation (1) pooled across all geographic strata. For the northern offshore spotted dolphins, this yielded an abundance estimate of 1,497,200 animals with a CV of 0.158. Although the estimate is very precise, it may be biased upwards because encounter rates were highest in the inshore stratum (Table 1) which received 42% of the total survey coverage but only represented 30% of the total geographic area.

We calculated school density using schools of all dolphin species; then calculated the proportion of those schools which were target species; and finally calculated the proportions of individuals of each species in the target species [equation (1)]. However, two alternate methods were investigated. They were to (1) calculate school density using only schools of target species and prorating to each species and (2) calculate abundance estimates using only data for each individual species. Method 1 does not require calculation of the proportion of all schools that are target schools, however, it utilises smaller samples than our method and a proportion of the unidentified schools must be allocated to the perpendicular distance distribution to calculate school density. We calculated the proportion of identified target schools in each perpendicular distance interval and then assigned that proportion of the unidentified schools detected in the interval to that interval.

Method 2 does not require calculation of species proportions but it utilises very small data sets. Sufficient data only exists to calculate estimates for spotted and spinner dolphins. In this method, we assumed no unidentified dolphin schools contained spotted dolphins.

Estimates of northern offshore spotted dolphins using methods 1 and 2 were 1,235,300 (CV 0.265) and 1,119,600 (CV 0.320) animals, respectively. The estimate for method 2 may have been smaller than both the method 1 estimate and our estimate of 1,275,400 animals using all dolphin schools (Table 2) because it did not include any unidentified schools. However, based on field experience the senior author believes that spotted dolphin schools rarely are not identified. CV estimates were similar for method 1 and our method (0.265 and 0.262, respectively) but both were smaller than the method 2 CV (0.320) which was based on small samples.

Abundance estimates calculated using all dolphin species and data pooled over all strata (total area in Table 1) may provide the most consistent *relative* abundance estimates during the six surveys. The method provides very precise estimates (CV for northern offshore spotted dolphins was 0.158 compared to our estimate of 0.262) because it avoids calculating estimates using small sample sizes. However, the abundance estimates may be biased upwards because proportionally more effort is expended in the high density inshore area (42%) compared to its relative size (30% of total survey area). This bias is acceptable if survey coverage among strata is relatively constant during all surveys as it was during the first two surveys. During 1986, the percents of the survey effort in the inshore, middle, west and south strata were 43, 28, 14 and 15%, respectively (Holt and Sexton, 1988a) and in 1987 they were 42, 30, 13 and 15%, respectively (Table 1).

The estimate of abundance for northern offshore spotted dolphins during 1987 was larger than the 1986 estimate. The 1986 and 1987 estimates were 929,000 (Holt and Sexton, 1988a) and 1,275,400 (Table 2) animals, respectively. These estimates were not statistically different ($p>0.01$). The larger 1987 estimate occurred because school density increased in 1987 in all strata. In addition, the proportion of spotted dolphins in the target species increased in the middle stratum. The 1986 estimates for density in the inshore, middle and west strata were 3.62, 2.56, and 1.89 schools/1000km^2, respectively (Holt and Sexton, 1988a); the corresponding 1987 estimates were 4.74, 3.15 and 2.16 schools/1000km^2, respectively (Table 1). The proportion of spotted dolphins of the target species in the middle stratum increased from 0.378 in 1986 to 0.524 in 1987. However, the proportion of all dolphins that were target species in the middle stratum slightly decreased from 0.906 in 1986 to 0.858 in 1987. In addition, school size estimates decreased slightly in the inshore and west strata and remained constant in the middle stratum. Estimates during 1986 in the inshore middle, and west strata were 89.41, 83.97 and 104.55 animals, respectively (Holt and Sexton, 1988a); in 1987 they were 81.57, 84.56 and 94.12 animals, respectively (Table 1).

The reason for the larger 1987 abundance estimate for northern offshore spotted dolphins may be attributed to sampling variability among surveys. Another factor is that dolphins in the south stratum during 1986 may have migrated into the northern strata during 1987. However, although the mean school size in the south stratum decreased from 179.04 animals (Holt and Sexton, 1988a) during the 1986 survey to 121.64 animals for 1987 survey (Table 1), the density estimate in the south stratum increased from 2.32 schools/1000km^2 in 1986 to 3.58 schools/1000km^2 in 1987. In addition, the proportion of target individuals that were spotted dolphins increased from 0.170 to 0.319. In fact, the abundance estimate for southern offshore spotted dolphins also increased (from 218,500 animals in 1986 to 501,800 animals in 1987).

Abundance estimates for the southern stocks varied greatly between 1986 and 1987. For example, the estimate for southern common dolphins was 943,200 animals during 1986 (Holt and Sexton, 1988a) but was 201,000 animals (Table 1) during 1987. This was because the proportion of common dolphins in the south stratum decreased from 0.661 during 1986 (Holt and Sexton, 1988a) to 0.080 during 1987 (Table 1). Estimates for the other species exhibited corresponding changes. This variability was because estimates in the south stratum were based upon few sightings. During 1986 and 1987, only 27 and 38 target schools, respectively, were detected in the south stratum. Species proportions in the west stratum were also based on few schools (Table 1) which may have yielded variable estimates for the western stocks.

Although estimates for some stocks varied greatly between years, the abundance estimates for all target species summed were similar. The 1986 and 1987 estimates for all target species were 4,471,200 (Holt and Sexton, 1988a) and 5,185,600 (Table 2) animals, respectively. The 1987 estimate is 16% larger than the 1986 estimate.

Selection of the best option to determine population changes will be investigated with additional years' data. We will also investigate several factors which may have contributed to differences observed between surveys. These include ship effects, observer variability, sea state effects and survey coverage variability (Holt and Cologne, 1987).

ACKNOWLEDGEMENTS

The cruises were successfully executed through the dedication of the ships' officers and crew. The data were collected by S. Beavers, S. Benson, C. Bisbee, C. Fried, W. Irwin, R. LeDuc, R. Pitman, J. Raffetto, K. Rittmaster, S. Sinclair, D. Skordal and M. Webber; they are dedicated professionals who spent many hours searching for marine mammals. P. Stangl contributed to the cruise logistics and observer training. We wish to thank J. Barlow, D. DeMaster, E. Edwards, A. Hohn, A. Jackson and M. Webber for serving as Cruise Leaders and for their exceptional dedication to collecting quality data. Finally, we thank I. Barrett, J. Carr and D. DeMaster for their support during the entire cruise preparation and execution. The data analyses were completed using a CRAY X-MP48 at the San Diego Supercomputer Center.

REFERENCES

Au, D., Perryman, W.L. and Perrin, W. 1979. Dolphin distribution and the relationship to environmental features in the eastern tropical Pacific. Southwest Fish. Cent. Adm. Rep. No. LJ-79-43. 59pp

Barlow, J. and Holt, R.S. 1986. Proportions of species of dolphins in the eastern tropical Pacific. US Dep. Commer., NOAA-TM-NMFS-SWFC-56. 44pp.

Buckland, S.T. 1985. Perpendicular distance models for line transect sampling. *Biometrics* 41: 177–95.

Burnham, K., Anderson, D. and Laake, J. 1980. Estimation of density from line transect sampling of biological populations. *Wildl. Monogr.* No. 72: 202pp.

Crain, B., Burnham, K., Anderson, D. and Laake, J. 1979. *A Fourier Series Estimator of Population Density for Line Transect Sampling*. Utah State Univ. Press, Logan. 25pp.

Drummer, T.D. 1985. Size-bias in line transect sampling. PhD Dissertation, Univ. Wyoming, Laramie, WY.

Hayes, R.J. and Buckland, S.T. 1983. Radial distance models for the line transect method. *Biometrics* 39: 29–42.

Holt, R.S. 1985. Estimates of abundance of dolphin stocks taken incidentally in the eastern tropical Pacific yellowfin tuna fishery. Southwest Fish. Cent. Adm. Rep. No. LJ-85-20. 32p.

Holt, R.S. 1987. Estimating density of dolphin schools in the eastern tropical Pacific ocean by line transect methods. *Fish. Bull., US* 85(3):419–34.

Holt, R.S. and Cologne, J.B. 1987. Factors affecting line transect estimates of dolphin school density. *J. Wildl. Manage.* 51(4):836–73.

Holt, R.S., Gerrodette, T. and Cologne, J.B. 1987. Research vessel survey design for monitoring dolphin abundance in the eastern tropical Pacific. *Fish. Bull., US* 85(3): 435–46.

Holt, R.S. and Jackson, A. 1988. Report of a marine mammal survey of the eastern tropical Pacific aboard the Research Vessel *McArthur* July 30 – December 10, 1986. US Dep. Commer., NOAA-TM-NMFS-SWFC-116. 143pp.

Holt, R.S. and Powers, J.E. 1982. Abundance estimation of dolphin stocks in the eastern tropical Pacific yellowfin tuna fishery determined from aerial and ship surveys to 1979. US Dep. Commer., NOAA-TM-NMFS-SWFC-23. 95pp.

Holt, R.S. and Sexton, S.N. 1988a. Monitoring trends in dolphin abundance in the eastern tropical Pacific using research vessels over a long sampling period: Analyses of 1986 data. In Review. (submitted to Fish. Bull.).

Holt, R.S. and Sexton, S.N. 1988b. Report of a marine mammal survey of the eastern tropical Pacific aboard the Research Vessel *David Starr Jordan* August 8 – 10 December, 1987. US Dep. Commer., NOAA-TM-NMFS-SWFC-117. 137pp.

Perrin, W.F., Scott, M.D., Walker, G.J. and Cass, V.L. 1984. Review of geographical stocks of tropical dolphins (*Stenella spp.* and *Delphinus delphis*) in the eastern Pacific. Southwest Fish. Cent. Adm. Rep. No. LJ-87-02. 68pp.

Richey, C.R. 1976. Memorandum of opinion. CA NO. 74–1465 and CA NO. 75–0227 US District Court, District of Columbia, May 11, 1976.

Smith, T.D. 1979. Report of the status of the porpoise stock workshop (August 27–31, 1979, La Jolla, CA). Southwest Fish. Cent. Adm. Rep. No. LJ-79-41. 120pp.

8929

Japanese Journal of Ichthyology
Vol. 36, No. 3 1989

魚類学雑誌
36巻3号 1989年

First Record of the Bigeye Sand Tiger Shark *Odontaspis noronhai* from the Pacific Ocean

Robert L. Humphreys, Jr.,
Robert B. Moffitt and Michael P. Seki

(Received December 11, 1988)

The family Odontaspididae consists of the genera *Eugomphodus* Gill, 1862 and *Odontaspis* Agassiz, 1838 (Compagno, 1984a). Two species of *Odontaspis* are currently recognized: *O. ferox* and *O. noronhai* (Compagno, 1984a). Compagno (1981) originally suggested that *O. noronhai* may be an extreme variant of *O. ferox*. Further evidence convinced Compagno (1984a, b) that *O. noronhai* is morphologically distinct from *O. ferox* and is a valid species.

Odontaspis noronhai was previously reported with certainty from only the Atlantic Ocean: 2 specimens from the type locality Madeira (Maul, 1955), 10 specimens from off southern Brazil (Sadowsky et al., 1984), and a specimen from the western Gulf of Mexico (Branstetter and McEachran, 1986). The single record outside of the Atlantic is either from the Indian Ocean or possibly South China Sea and based on a set of jaws nearly identical to the holotype in dentition (pers. comm. cited in Sadowsky et al., 1984). Furthermore, several *Odontaspis* teeth collected from bottom deposits in the central North Pacific, although not clearly identifiable to *O. noronhai*, suggest a possible Pacific occurrence (Belyaev and Glikman, 1970 as cited in Sadowsky et al., 1984). Herein, we report the first definitive record of *O. noronhai* from the Pacific Ocean and compare its morphometrics and dentition with those reported elsewhere.

Materials and methods

A 216.8 cm total length (TL) male *O. noronhai* was captured on tuna longline gear set by a commercial vessel fishing 550 km southwest of the Island of Hawaii (16°N, 160°W) in July 1985. Depth of capture is uncertain; the vessel captain estimated a 450 m depth. Stored frozen for 1 year, the specimen was partially dehydrated when measured. This specimen was deposited in the Laboratory of Marine Zoology, Hokkaido University (HUMZ 110959) in Hakodate, Hokkaido, Japan. Measurements were taken to the nearest millimeter following Compagno (1984a) and converted to percent total length (%TL) to compare with Atlantic specimens (Maul, 1955; Sadowsky et al., 1984; Branstetter and McEachran, 1986). The repositories of the Atlantic specimens are the Museu Municipal do Funchal (MMF), Museu de Pesca (MP), and the Texas Cooperative Wildlife Collections (TCWC).

Tooth count of the Hawaii specimen follows the methods and terminology of Applegate (1965), except for the necessity of combining counts of lateral and posterior teeth. This modification still allowed for a comparison of dental counts between our Hawaii specimen and those from the Altantic reported in Sadowsky et al. (1984) and Barnstetter and McEachran (1986).

Odontaspis noronhai (Maul, 1955)
(Fig. 1)

Carcharius noronhai Maul, 1955: 3, figs. 1–4 (type locality, off Camara de Lobos, Madeira).

Odontaspis noronhai: Sadowsky et al., 1984: 69, figs. 1–4 (southern Brazil and Indian Ocean or possibly South China Sea): Branstetter and McEachran, 1986: 153, fig. 1 (Gulf of Mexico).

Description. Proportional dimensions and dental counts of the Hawaii and Atlantic specimens of *O. noronhai* are presented in Tables 1 and 2, respectively. The following description is of the 216.8 cm TL male Hawaii specimen.

Snout conical and bulbous, tip rounded. Preoral length (snout tip to mouth) 21.7% of head length (snout tip to last gill-slit). Eyes large and ovoid, nictating membrane absent. Spiracle small, located behind and slightly below level of lower eye border. Mouth extends just beyond posterior border of eye. Snout tip to pectoral origin 82.1% of distance between first and second dorsal origins. Origin of first dorsal aligned behind inner margin of pectorals. Origin of second dorsal over pelvic inner margin, second dorsal insertion aligned somewhat closer to anal origin than pelvic insertion. Anal fin low and rounded, outer portion of posterior free margin under precaudal pit. First dorsal slightly larger than pelvics, second dorsal smaller than pelvics, and anal smaller than second

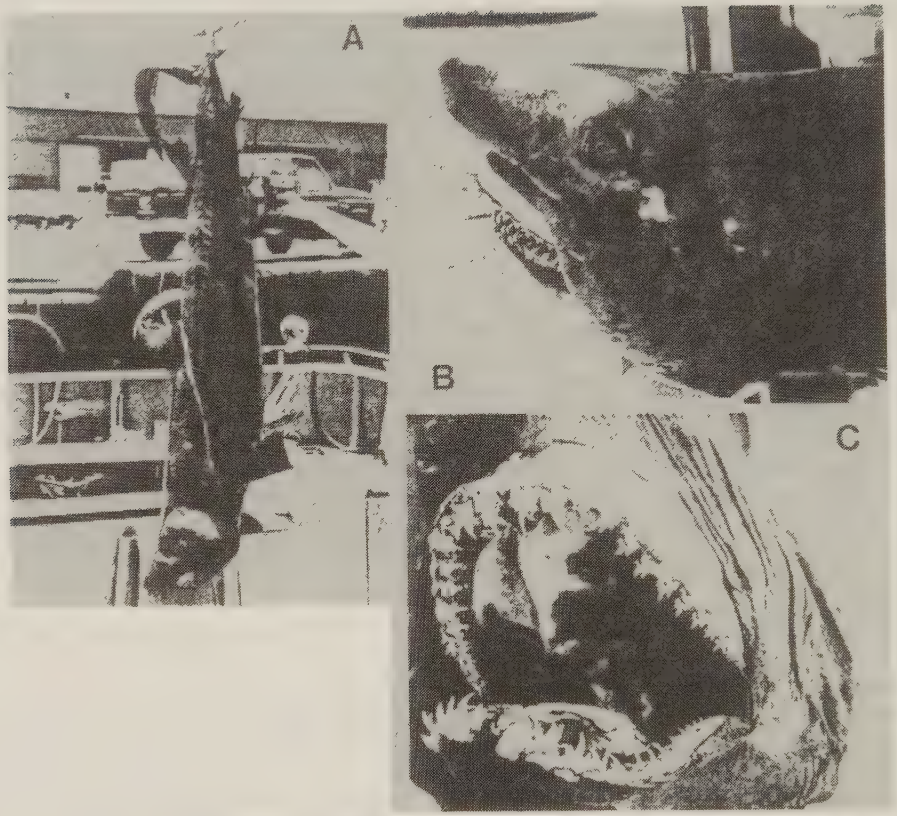


Fig. 1. *Odontaspis noronhai*, HUMZ 110959, 216.8 cm total length male, from off the Island of Hawaii. A: Lateral view. B: Lateral view of head. C: Upper and lower jaw; note dark coloration on palate and along inner lining of upper jaw.

dorsal. Lateral keels absent. Tip of ventral caudal lobe somewhat pointed. Edge along posterior margin of all fins appears thin and frayed.

Single symphyseal tooth in upper jaw and first two symphyseal teeth on either side of lower jaw without cusplets. Third and fourth symphyseal teeth of lower jaw with minute cusplet on lateral side only. Anterior, intermediate, and lateral teeth in both jaws similar with a distinct, pointed cusplet on each side of cusp; slender, curved and awl-shaped; teeth appear to protrude outward from jaws. Anterior teeth longest, those of lower jaw somewhat longer than those of upper. In both upper and lower jaws, teeth following 1st lateral gradually decrease in size.

Body color a uniform chocolate brown, all fins except pectorals with a thin dark edging along posterior margin. Inside mouth, inner lining of both jaws black; an irregular-shaped, dark patch present on middle of palate and tongue; internal gill arches with dark patches.

Discussion

Proportional dimensions of our Hawaii specimen closely correspond with those of the intact Brazil (MP 547) and Gulf of Mexico specimens with only a few differences. The Hawaii specimen has a somewhat greater upper caudal fin and anterior pectoral margin length than the Brazil specimen and a greater prepectoral but smaller presecond dorsal length than the Gulf of Mexico specimen. The smaller outer clasper length of the Hawaii specimen is attributed to sexual immaturity. Greatest differences exist between the

Table 1. Proportional dimensions (in percent of total length (TL)) of Hawaiian *Odontaspis noronhai*, two Madeira specimens including holotype (MMF 2691) (Maul, 1955), two Brazil specimens (Sadowsky et al., 1984), and Gulf of Mexico (Branstetter and McEachran, 1986) specimen. The Brazil (uncat.) specimen consists of only a head; TL was estimated, so %TL values for this specimen are approximations.

Measurement	Hawaii, male HUMZ 110959 216.8 cm TL		Madeira, female MMF 2691 171 cm TL	Madeira (sex?) MMF 3376 118 cm TL	Brazil, male MP 547 342 cm TL	Brazil (sex?) (uncat.) ca. 360 cm TL	Gulf of Mexico, female TCWC 3922.1 321 cm TL
	cm	%TL	%TL	%TL	%TL	%TL	%TL
Snout tip to:							
outer nostrils	10.8	5.0	—	—	—	—	—
eye	15.6	7.2	5.9	6.3	5.7	ca. 5.9	7.0
mouth	10.9	5.0	5.0	7.0	4.4	ca. 4.7	5.3
spiracle	24.7	11.4	12.6	—	9.8	ca. 10.9	—
1st gill-slit	36.4	16.8	19.0	—	16.0	—	—
5th gill-slit	50.3	23.2	24.0	—	23.5	—	—
pectoral origin	51.2	23.6	22.6	24.1	22.8	—	20.9
pelvic origin	115.4	53.2	51.7	50.2	52.6	—	53.9
1st dorsal origin	68.8	31.7	30.4	31.6	31.3	—	33.1
2nd dorsal origin	130.5	60.2	55.0	57.9	59.6	—	62.6
anal fin origin	145.2	67.0	62.0	63.8	68.1	—	67.6
upper caudal origin	159.1	73.4	68.4	71.8	73.7	—	72.9
Distance between origins of:							
1st and 2nd dorsal fins	62.4	28.8	—	—	—	—	—
pectoral and pelvic fins	70.2	32.4	28.6	26.0	—	—	33.0
pelvic and anal fins	30.2	13.9	11.7	14.3	—	—	13.7
Space between:							
dorsal fin bases	39.9	18.4	16.5	15.5	—	—	19.9
2nd dorsal and caudal fins	16.1	7.4	—	—	—	—	—
pectoral and pelvic fins	59.4	27.4	—	—	—	—	—
pelvic and anal fins	16.7	7.7	—	—	—	—	—
anal and caudal fins	7.5	3.5	—	—	—	—	—
Eye:							
Horizontal diameter	4.9	2.3	2.8	2.3	1.8	ca. 1.7	1.6
Eye-spiracle distance	6.8	3.1	—	—	3.4	ca. 3.1	—
Interorbital space	10.8	5.0	5.0	—	4.5	ca. 4.7	—
Distance between inner corners of nostrils	9.0	4.2	4.9	4.3	3.7	ca. 4.1	4.7
Mouth length	10.4	4.8	—	—	3.7	ca. 5.3	—
Gill height:							
1st gill-slit	14.6	6.7	5.5	5.0	5.1	—	5.6
3rd gill-slit	12.8	5.9	5.1	4.6	—	—	5.9
5th gill-slit	12.8	5.9	4.9	3.9	4.8	—	4.7

Table 1. Continued.

Measurement	Hawaii, male HUMZ 110959 216.8 cm TL		Madeira, female MMF 2691 171 cm TL	Maderia (sex?) MMF 3376 118 cm TL	Brazil, male MP 547 342 cm TL	Brazil (sex?) (uncat.) ca. 360 cm TL	Gulf of Mexico, female TCWC 3922.1 321 cm TL
	cm	%TL	%TL	%TL	%TL	%TL	%TL
1st dorsal fin:							
length	24.4	11.3	—	—	—	—	—
length of base	19.7	9.1	8.1	10.6	9.6	—	10.9
length of posterior margin	11.2	5.2	—	—	—	—	—
height	14.5	6.7	5.1	6.2	6.0	—	6.2
2nd dorsal fin:							
length	16.3	7.5	—	—	—	—	—
length of base	11.6	5.4	5.3	6.4	6.4	—	5.8
length of posterior margin	9.5	4.4	—	—	—	—	—
height	14.5	4.1	4.4	4.7	4.3	—	4.4
Anal fin:							
length	11.9	5.5	—	—	—	—	—
length of base	7.9	3.6	3.3	5.2	3.5	—	3.9
length of posterior margin	7.2	3.3	—	—	—	—	—
height	5.3	2.4	2.8	4.5	3.1	—	4.1
Pectoral fin:							
length of base	11.1	5.1	—	4.9	4.6	—	5.1
length of anterior margin	30.4	14.0	12.5	12.7	11.6	—	15.3
length of inner margin	11.0	5.1	4.0	4.9	4.2	—	6.9
length of posterior margin	19.3	8.9	—	—	—	—	—
height	23.9	11.0	9.8	8.0	—	—	12.8
Pelvic fin:							
length	23.4	10.8	—	—	11.4	—	—
length of base	13.6	6.3	—	—	7.9	—	—
length of anterior margin	18.6	8.6	9.4	7.9	7.5	—	9.5
length of posterior margin	19.9	9.2	5.4	7.0	—	—	8.4
height	14.3	6.6	—	—	—	—	5.6
length of inner margin	11.8	5.4	—	—	—	—	—
Clasper:							
outer length	3.6	1.7	—	—	8.9	—	—
inner length	15.4	7.1	—	—	—	—	—
base width	1.3	0.6	—	—	—	—	—
Caudal fin:							
length of upper lobe	64.5	29.8	29.2	28.1	26.3	—	29.3
length of lower lobe	21.0	9.7	—	—	8.5	—	11.1
depth of notch	5.0	2.3	—	—	—	—	—
subterminal caudal margin	6.3	2.9	—	—	—	—	—

Madeira holotype (MMF 2691) and the Brazil (MP 547), Gulf of Mexico, and Hawaii specimens. Three of the holotype's proportional dimensions (preanal, pre-second dorsal, and precaudal length) were 4.5–7.6%TL smaller than those of the Hawaii, Brazil (MP 547), and Gulf of Mexico specimens. Allometric growth and/or possible taxidermic alteration of the holotype may be factors responsible for these discrepancies. Other variation from the holotype morphology involves the alignment of the second dorsal origin just anterior to the pelvic midbase. This was originally described by Maul (1955) and is one of the three key characters proposed by Compagno (1984a) to distinguish *O. noronhai* from *O. ferox*. The second dorsal origin appears to be aligned over the posterior third of the pelvic fin base in the Brazil (MP547) and Gulf of Mexico specimens and is aligned over the pelvic inner margin of the Hawaii specimen. The apparent variability of this morphological feature diminishes its utility as an identifying characteristic.

We also found an apparent error on page 3 in Maul (1955) regarding head length: "Eye moderate, almost 2.7 in snout, which is nearly 4 in head (measured from snout tip to last gill-slit)." On page 4 of Maul (1955), nine body measurements (in millimeters) of the holotype are presented. Assuming that the measurement snout tip to upper lip in Maul (1955) refers to snout length, this length divided into snout tip to last gill-slit length yields a value of 4.8, whereas snout length divided into snout tip to first gill-slit length yields 3.8. We believe Maul (1955) mistakenly used the latter measurement for head length in the above cited text.

Another character proposed by Compagno (1984a) to distinguish *O. noronhai* from *O. ferox* is the presence of only a single row of intermediate teeth on each side of the upper jaw. The holotype and all other *O. noronhai* examined by Sadowsky et al. (1984) and Branstetter and McEachran (1986) concur with Compagno (1984a). The Hawaii specimen, however, possesses two rows of upper intermediate teeth on each side. Other dentitional differences in the Hawaii specimen include the presence of four rows of lower symphyseal teeth and three rows of lower anterior teeth on each side compared with two to three rows of lower symphyseals and two rows of lower anteriors in all other *O. noronhai* examined (Sadowsky et al., 1984; Branstetter and McEachran, 1986). Recognizing that the third lower anterior tooth of the Hawaii specimen might also be classified as a 1st lateral tooth by other investigators, we attribute the other dentitional differences to natural variation

Table 2. Tooth count and dental formula of Hawaiian *Odontaspis noronhai* with the revised count of the Madeira holotype and data from three Brazil specimens (Sadowsky et al., 1984) and one Gulf of Mexico specimen (Branstetter and McEachran, 1986). Dental formula follows Applegate (1965) where P = posterior, L = lateral, I = intermediate, A = anterior, and S = symphyseal teeth. Posterior and lateral tooth counts were combined for the Hawaii specimen.

Specimen	Tooth count (upper/lower)	Dental formula (upper/lower)									
Hawaii,	36	P ⊥	L-14	I-2	A-2	S-1	S-0	A-2	I-2	L +	P-13
(HUMZ 110959)	46	P ⊥	L-16	I-0	A-3	S-4	S-4	A-3	I-0	L +	P-16
Madeira,	38										
(MMF 2691)	44										
Brazil,	38	P-3	L-13	I-1	A-3	S-0	S-0	A-2	I-1	L-13	P-3
(MP 547)	42	P-3	L-13	I-0	A-2	S-3	S-3	A-2	I-0	L-13	P-3
Brazil,	40	P-4	L-13	I-1	A-2	S-0	S-0	A-2	I-1	L-13	P-4
(uncat.)	43	P-4	L-13	I-0	A-2	S-3	S-3	A-2	I-0	L-13	P-3
Brazil,	43	P-4	L-13	I-1	A-2	S-1	S-0	A-2	I-1	L-13	P-6
(MM 250)	40	P-4	L-12	I-0	A-2	S-2	S-2	A-2	I-0	L-12	P-4
Gulf of Mexico,	34	P-4	L-10	I-1	A-2	S-0	S-0	A-2	I-1	L-10	P-4
(TCWC 3922.1)	37	P -	L ·	I –	A-16	S-2	S-2	17-A	– I	– L	– P

between ocean populations and believe they do not warrant separate taxonomic status for the Hawaii specimen.

Despite variation in two diagnostic features, *O. noronhai* is distinguishable from *O. ferox* by several characters. *Odontaspis noronhai* has only one cusplet on each side of a cusp, one to two rows of upper intermediate teeth between anterior and lateral rows, two to four rows of lower symphyseal teeth on each side, and uniform chocolate brown to dark reddish brown body coloration, without spots.

Few aspects of the habits and ecology of *O. noronhai* are known. Sadowsky et al. (1984) suggested that the capture of the large Brazil specimens, all from the same area and only during the spring season, may reflect a migrational movement. Observations of the Hawaii specimen at time of capture indicate highly aggressive behavior; the shark vigorously thrashed and snapped while at the surface and on deck (D. Knottingham, pers. comm.). Vertical distribution is extensive, ranging from 60–120 m off Brazil (Sadowsky et al., 1984) to 800–1,000 m off Madeira (Maul, 1955). Atlantic captures of *O. noronhai* suggest this species is a coastal inhabitant, although the Hawaii specimen was caught over deep oceanic waters far offshore. Interestingly, *O. noronhai* was not reported among some 6,000 sharks captured during an extensive longline fishing program conducted throughout the central Pacific in 1952–1955 (Strasberg, 1958). Fishing depths surveyed ranged from the surface to 150 m, which suggests that *O. noronhai* probably inhabits deeper waters in the central Pacific. The previously unknown occurrence of *O. noronhai* in the Pacific, coupled with the capture of all known *O. noronhai* by commercial fishing gear, underscores the important contribution that fishermen can offer in furthering our knowledge of rare and new species.

Acknowledgments

We thank Captain Don Knottingham and the crew of the Stacey Ann for the collection and donation of this specimen. J. Seigel and L. Compagno reviewed the manuscript and offered valuable comments.

Literature cited

Applegate, S. H. 1965. Tooth terminology and variation in sharks with special reference to the sand shark, *Carcharias taurus* Rafinesque. Contr. Sci. Los Angeles County Mus., 86: 1–18.

Belyaev, G. M. and L. S. Glikman. 1970. The teeth of sharks on the floor of the Pacific Ocean. Trans. P. Shirshov Inst. Oceanol., Acad. Sci. USSR, Moscow, 88: 252–276. (In Russian with English summary.)

Branstetter, S. and J. D. McEachran. 1986. A first record of *Odontaspis noronhai* (Lamniformes: Odontaspidae) for the western North Atlantic, with notes on two uncommon sharks from the Gulf of Mexico. Northeast Gulf Sci., 8 (2): 153–160.

Compagno, L. J. V. 1981. Sharks. *In* W. Fischer, G. Bianchi and W. B. Scott, eds. FAO species identification sheets for fishery purposes. Eastern Central Atlantic. Fishing Areas 34, 47 (in part), Vol. 5. By arrangement with FAO, Rome. Department of Fisheries and Oceans, Ottawa.

Compagno, L. J. V. 1984a. FAO species catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1. Hexanchiformes to Lamniformes. FAO Fish. Synop., No. 125, vol. 4, pt. 1: 1–249.

Compagno, L. J. V. 1984b. Sharks. *In* W. Fischer and G. Bianchi, eds. FAO species identification sheets for fishery purposes. Western Indian Ocean. Fishing Area 51, Vol. 5. Prepared and printed with the support of the Danish International Development Agency (DANIDA). FAO, Rome.

Maul, G. E. 1955. Five species of rare sharks new for Madeira including two new to science. Notul. Nat. Acad. Nat. Sci. Philad., (279), 13 pp.

Sadowsky, V., A. F. Amorim and E. A. Arfelli. 1984. Second occurrence of *Odontaspis noronhai* (Maul, 1955). B. Inst. Pesca, Sao Paulo, 11(1): 69–74.

Strasberg, D. W. 1958. Distribution, abundance, and habits of pelagic sharks in the central Pacific Ocean. Fish. Bull., U. S. Fish. Wildl. Serv., 58: 335–361.

(Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822–2396, U.S.A.)

ミズワニ科 *Odontaspis noronhai* の太平洋初記録

Robert L. Humphreys, Jr.・Robert B. Moffitt・Michael P. Seki

ミズワニ科シロワニ属の *Odontaspis noronhai* はこれまで大西洋からのみ報告されていた (holotype のものとほとんど同じ歯列をもつインド洋あるいは南シナ海でとれたと思われる一組の顎の報告はある). 今回ハワイ島の南西 550 km の地点でマグロ延縄にかかった個体が採集されたので，その測定値と歯列について他海域のものと比較し報告する．標本は北海道大学水産学部に保管されている．

8930

Copeia, 1989(1), pp. 142–153

Synonymy and Life History of the North Pacific Pelagic Armorhead, *Pseudopentaceros wheeleri* Hardy (Pisces: Pentacerotidae)

Robert L. Humphreys, Jr., Gary A. Winans
and Darryl T. Tagami

Specimens of the nominal species *Pseudopentaceros wheeleri* Hardy and *P. pectoralis* Hardy were examined morphologically and electrophoretically to test the validity of the two species. Samples were collected primarily from the Hancock Seamounts of the southern Emperor–northern Hawaiian Ridge as well as from the North Pacific open ocean and northwestern Hawaiian Islands. Morphometric results indicate continuity between *P. wheeleri* and *P. pectoralis*. No evidence of species separation was revealed in analyses of meristic and electrophoretic data. We conclude that the North Pacific pelagic armorhead consists of a single, metamorphic species, which we, as first revisers, elect to call *P. wheeleri*. A hypothesis is proposed that attributes morphological variation to different life-history stages.

THE pelagic armorhead, so named for its offshore occurrence and rough, bony head plates (Follett and Dempster, 1963) has been recorded from the North and South Pacific, South Atlantic, and southern Indian oceans (Borets, 1980; Kotlyar, 1982) as *Pentaceros richardsoni* Smith. Centers of abundance and reproduction coincide with seamounts of the southern Emperor–northern Hawaiian Ridge (SE-NHR) in the central North Pacific and the Walvis Ridge in the South Atlantic (Borets, 1980). Reports of the Japan Fisheries Agency (1974), Sasaki (1974), and Takahashi and Sasaki (1977) documented morphological variation among SE-NHR pelagic armorhead but all still recognized a single species. These reports described three morphotypes at the seamounts based on relative body depth (BDEPTH) and coloration: "lean," "intermediate," and "fat" (Fig. 1a–c).

The lean and intermediate types are brownish in coloration, and predominate in catches at the SE-NHR seamounts. In contrast, the fat type is bluish gray, and is only infrequently caught at the SE-NHR seamounts; it is also the only morphotype found in the open ocean of the North Pacific. Coloration of the fat type of armorhead also differs by region: those from the open ocean (Fig. 1d) are dorsally mottled and have more prominent countershading (bluish dorsally and whitish ventrally) than those from the SE-NHR. Data (Humphreys, unpubl.) indicate an intergradation in BDEPTH from fat to intermediate and from intermediate to lean, with the former pair occasionally also exhibiting intergraded coloration. Large adult specimens (Fig. 1e) resembling the seamount intermediate type in relative BDEPTH and coloration have recently been recorded from the northwestern Hawaiian Islands (NWHI). This large adult type is the only morphotype present in this region and has not been recorded elsewhere in the North Pacific Ocean (Tagami and Humphreys, unpubl.).

A revision of the family Pentacerotidae (Hardy, 1983) placed the pelagic armorhead in the genus *Pseudopentaceros* and recognized three species. Two, *P. wheeleri* and *P. pectoralis*, were said to inhabit the North Pacific Ocean, and the third, *P. richardsoni*, to be restricted to waters in the temperate Southern Hemisphere. *Pseudopentaceros wheeleri* was primarily distinguished from *P. pectoralis* by a smaller BDEPTH (expressed as SL/BDEPTH) and, secondarily, by a greater head length/least bony interorbital width (HL/IO). The two species were considered partially sympatric in the central North Pacific. Hardy (1983) gave the range of *P. wheeleri* as Japan to Hawaii and of *P. pectoralis* as Hawaii to the Aleutian Islands and east to the North American coast.

In this paper, morphological and electrophoretic variation are described for over 300 specimens of the pelagic armorhead from the SE-NHR seamounts, NWHI, and North Pacific open ocean. The material available to Hardy (1983) included only a small collection of SE-NHR lean type and lacked the SE-NHR inter-

© 1989 by the American Society of Ichthyologists and Herpetologists

mediate and fat types. With a more complete set of morphotypes, we examine the concordance of morphological and electrophoretic characters to the model of Hardy (1983). Our results lead to an alternate explanation of variation in pelagic armorhead.

Materials and Methods

Morphometrics and meristics.—Specimens were collected from Northwest Hancock Seamount (30°16′N, 178°43′E) and Southeast Hancock Seamount (29°48′N, 179°04′E), which are guyots located at the southern end of the SE-NHR (Fig. 2). Each guyot has a summit depth and diameter of 260 m and approx. 2 km, respectively. Specimens were collected from bottom trawl operations aboard the Japanese vessel KITAKAMI MARU during 1 Aug.–15 Oct. 1981 and from bottom handline and trawl operations conducted aboard the NOAA ship TOWNSEND CROMWELL during 19 Oct.–2 Dec. 1982 and 2 June–27 July 1983. These specimens are currently uncatalogued and held at the Southwest Fisheries Center (SWFC), Honolulu Laboratory. Other specimens used in this study are listed.

Specimens collected at the Hancock Seamounts for morphological analysis only were frozen whole at −20 C and later fixed in 10% formalin and stored in 70% ethyl alcohol. Prior to preservation, whole body weight was taken to the nearest gram. Fork length (FL) and SL measurements were taken on a metric board. A vernier caliper was used to measure BDEPTH, HL, IO, width at base of pelvic spine, pectoral-fin length, greatest orbital length, and length from posterior of dorsal-fin base to posterior of anal-fin base. Measurements were taken to the nearest millimeter, duplicating the methods of Hardy (1983).

Species identification followed the SL/BDEPTH criteria of 2.4–2.9 and 3.1–4.0 for *P. pectoralis* and *P. wheeleri*, respectively, in the species key to Pentacerotidae in Hardy (1983). Condition factor (CF) was calculated by the formula

$$\mathrm{CF} = \text{body weight (g)} \times 10^{5} \times \mathrm{SL}^{-3}\,\text{(mm)}$$

Here, CF is used as a relative index of "fatness" because fat content was not measured.

Counts taken follow the methods of Hubbs and Lagler (1958): dorsal-fin spines; dorsal-fin rays; anal-fin spines; anal-fin rays; pectoral-fin rays; lateral-line scales in SL; scale rows below

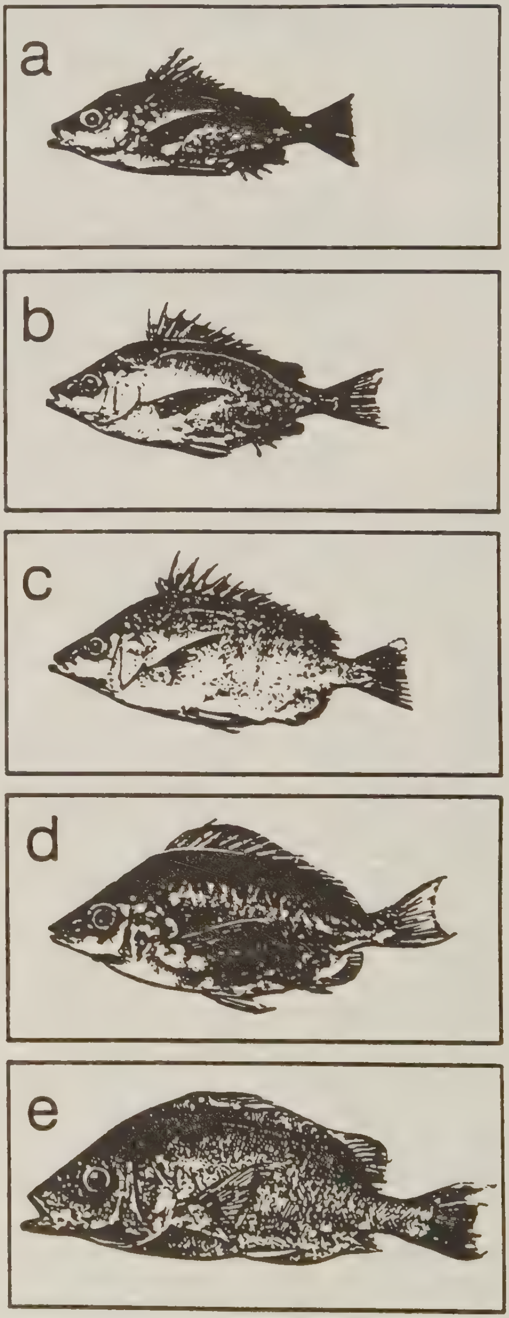


Fig. 1. Specimens representing: a) lean; b) intermediate; c) fat; d) open ocean fat; and e) large adult morphotypes of *Pseudopentaceros wheeleri*.

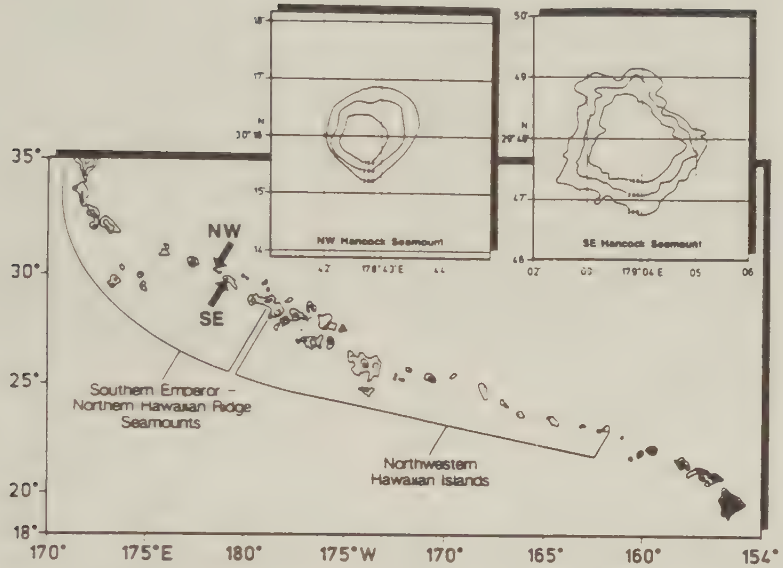


Fig. 2. Locations of Northwest and Southeast Hancock Seamounts in relation to other seamounts and elevated features of the southern Emperor–northern Hawaiian Ridge and Northwestern Hawaiian Islands. Bathymetric contours are in fathoms.

lateral line; midline scales from isthmus to pelvic-fin insertion; upper, lower, and total gill rakers on first gill arch; and precaudal, caudal, and total vertebrae. Counts were made by a dissecting microscope; flesh was removed for vertebral counts.

Possible meristic differences between species were tested by contingency table analysis. Frequency cells were combined when an expected frequency was <1 in any cell or <5 in 20% of the cells (Zar, 1984). Means of open ocean fat and large adult types were not tested because of small sample sizes.

Electrophoresis.—Fish for electrophoretic analysis were obtained from bottom handline and bottom trawl operations at the Hancock Seamounts during 12–29 July 1984 on the TOWNSEND CROMWELL. Samples of eye, heart, liver, and dorsal muscle were taken within 2 h of capture from 128 lean, 75 intermediate, and 20 fat types. Tissues were stored at −20 C until analysis. Carcasses were saved for later morphological verification and species identification.

Tissue extracts were subjected to starch gel electrphoresis by standard electrophoretic procedures. On the gels, 26 enzymes (encoding 39 loci) were identified by specific histochemical staining procedures as described in Shaw and Prasad (1970), Allendorf et al. (1977), or as given in Table 1. Electrophoretic conditions for resolving the 39 loci are presented in Table 1. General assumptions for interpreting electrophoretic data are described in Utter et al. (1987).

Standard electrophoretic nomenclature was used for the loci and alleles (Utter et al., 1987). Multiple loci for an enzyme were designated with hyphenated numerals, with the locus encoding for the least anodal (i.e., closest to the origin) homomer designated as one, the next as two, and so on. Alleles were scored numerically, with the most common allele at a locus designated as 100. Other alleles were assigned numbers representing the mobility of their homomeric protein relative to the migration of that most common.

The amount of electrophoretic variability at a locus in a sample was measured as heterozygosity (h), defined as $h = 1 - \sum x_i^2$, where x_i is the frequency of the ith allele at the locus. The amount of variability in a sample combining all loci was estimated as the average heterozygosity per locus (H), where H is the mean h combining all loci examined in a sample.

Genetic differences among the groups were tested in two ways. First, differences in allele frequency were determined by standard chi-

TABLE 1. ENZYMES USED IN ELECTROPHORETIC SURVEY OF *Pseudopentaceros wheeleri*.

Enzyme (commission no.)	Abbreviation	No. of loci	Monomorphic (M) or polymorphic (P)	Tissue[a]	Electrophoresis buffer[b]
Acid phosphate (3.1.3.2)	Acp	1	M	L	AC
Aconitate hydratase (4.2.1.3)	Ah	3	P, M, M	L, Mu, Mu	TBE, AC, AC
Adenylate kinase (2.7.4.3)	Ak	1	M	H	AC
Alcohol dehydrogenase (1.1.1.1)	Adh	1	P	L	AC
Creatine kinase (2.7.3.2)	Ck	3	P, P, M	Mu, Mu, H	AC
Diaphorase (1.6.4.3)	Dia	1	M	L	TC/LB
Dipeptidase (3.4.13.11)	DPEP	1	M	Mu	TBE
Esterase[c] (3.1.1._)	Est	2	P, P	L	TC/LB
Fumarate hydratase (4.2.1.2)	Fh	1	M	L	TBE
Glucosephosphate isomerase (5.3.1.9)	Gpi	2	P, P	Mu	TC/LB
Glycerol-3-phosphate dehydrogenase (1.1.1.8)	G3phd	1	M	Mu	TBE
Guanine deaminase (3.5.4.3)	Gda	1	M	L	TC/LB
Isocitrate dehydrogenase (1.1.1.42)	Idh	1	P	H	AC
Lactate dehydrogenase (1.1.1.27)	Ldh	3	P; M, M	Mu; H	AC; AC-N
Lactoyl-glutathione lyase (4.4.1.5)	Lgl	1	M	Mu	TC/LB
Malate dehydrogenase (1.1.1.37)	Mdh	3	M, M, P	H	AC-N
Malate dehydrogenase (NADP⁺) (1.1.1.40)	Mdhp	1	M	H	AC
Mannosephosphate isomerase (5.3.1.8)	Mpi	1	P	H	TBE
Nucleosidetriphosphate pyrophosphate (3.6.1.19)	Ntp	1	P	Mu	TC/LB
Peptidase-LT (3.4._._)	Pep-lt	1	P	Mu	TBE
Phosphoglucomutase (2.7.5.1)	Pgm	1	P	Mu	TC/LB
6-phosphogluconate dehydrogenase (1.1.1.44)	Pgdh	1	P	H	AC
Phosphoglycerate kinase (2.7.2.3)	Pgk	1	P	H	AC-N
Proline dipeptidase (3.4.13.9)	Pdpep	1	P	L	TC/LB
Sorbitol dehydrogenase (1.1.1.14)	Sdh	1	P	L	TC/LB
Superoxide dimutase (1.15.1.1)	Sod	1	M	H	TC/LB
Tripeptide aminopeptidase (3.4.11.4)	Tapep	1	M	Mu	TBE
Tyrosine aminotransferase (2.6.1.5)	Tat	1	M	L	TC/LB
Xanthine oxidase (1.2.3.2)	Xo	1	M	L	TBE

[a] Mu = muscle; L = liver; H = heart.

[b] Buffers: AC described by Clayton and Tretiak (1972). Gel: 0.002 M citric acid, pH 6.0. Electrode: 0.04 M citric acid, pH 6.5. Both buffers are pH adjusted with N-(3-aminopropyl)-morpholine. AC-N is same as above except NAD⁺ is added to the gel (0.015%) and cathodal electrode chamber (0.03%). TC/LB described by Ridgway et al. (1970). Gel: Tris-0.005 M citric acid, pH 8.5. Electrode: 0.06 M lithium hydroxide-0.3 M boric acid, pH 8.1. Gels were made using 99% gel buffer and 1% electrode buffer. TBE described by Boyer et al. (1963). Gel: 0.036 M Tris, 0.02 boric acid, and 0.002 M EDTA, pH 8.7. Electrode: 0.1 M boric acid, 0.18 M Tris, and 0.01 M EDTA.

[c] Substrate for Est-1 is 4-methylumbelliferyl acetate; substrate for Est-2 is alpha-napthyl proprionate.

square contingency tables. For this analysis, rare alleles were pooled into a secondary allele class. Secondly, the observed genotype frequencies for each polymorphic locus were compared to the genotype frequencies expected under Hardy-Weinberg equilibrium for each morphotype separately, and then pooled over all morphotypes. Pooling independent gene pools may result in a deficiency of heterozygote genotypes, thereby yielding another test of the genetic independence of two or more samples (Turner and Grosse, 1980; Winans and Jones, 1988).

RESULTS

Morphometrics.—Of the 337 pelagic armorhead examined morphologically from several locations, the Hancock Seamount morphotype samples exhibited narrow distributions of SL (Table 2). The large distribution in SL in the open ocean fat type was due to the presence of both juvenile and adult specimens in our samples: juveniles were not present in the remaining morphotype samples.

The HL/IO, SL/BDEPTH, and CF data ex-

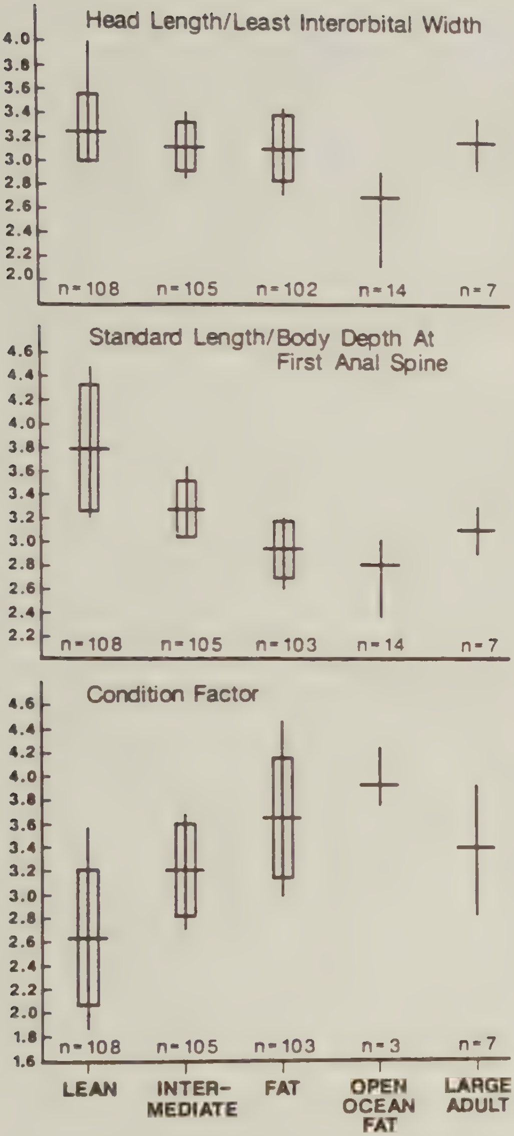


Fig. 3. Ratios of three morphological characters of *Pseudopentaceros wheeleri* separated by morphotype. Means are indicated by horizontal lines, 95% confidence limits are represented by boxes, and ranges are displayed as vertical lines. Confidence limits are not given for open ocean fat and large adult types.

hibited a continguous pattern of variation from open ocean fat type at one extreme to the lean type at the other (Fig. 3). The mean and range of variation among the large adult type samples were most similar to the intermediate type. The contiguous variation in CF paralleled our field observations of decreasing visceral fat content with "leaner" specimens. Other morphometric ratios showed no discrete range differences separating any one morphotype from all the rest. The morphotype samples assignable to *P. wheeleri* were as follows: all lean, 101 intermediate, 13 fat, and four large adult specimens. Specimens assignable to *P. pectoralis* included all the open ocean fat type, 66 of the fat type from the Hancock Seamounts, and two large adult specimens. The remaining specimens were not assignable to either species.

Meristics.—Contingency table analysis revealed no significant differences between morphotype means in 13 of 14 meristics examined ($P > 0.05$; Table 3). A significant difference in mean number of anal-fin rays occurred between fat type vs intermediate and lean types ($P = 0.01$). This difference, however, provided no distinct criteria for identifying fat type individuals from those of the intermediate and lean types. The limited data available on meristic frequencies of open ocean fat and large adult types indicated that they differ little from those of the Hancock Seamount morphotypes.

Electrophoresis.—Considerable levels of electrophoretic variation occurred at the 39 enzyme loci. Although no electrophoretic variation was detected at 20 loci, the remaining 19 loci had discernible protein variation. One or two heterozygotes were seen at Ck-2, Est-2, Ldh-1, Pgdh, Pgk-1, and Pdpep. For the remaining polymorphic loci, the frequency of the most common allele was <0.99 (Table 4). Eight of the loci in Table 4 were polymorphic at the 0.95 level. The most variable loci were Ah-1, Adh, Gpi-1, and Pgm for which average heterozygosity ranged from 0.36–0.58 and 4–5 alleles per locus were observed. Treated as a single group, pelagic armorhead had an average heterozygosity of 0.077 and average number of alleles per locus of 1.85. These relatively high levels of electrophoretic variability allowed for differences among the lean, intermediate, and fat types to be tested.

No significant differences between morphotypes were detected, as indicated by contingency table analysis of the allele frequency data (total $\chi^2 = 5.63$, df = 11, $P = 0.90$) and the individual and pooled tests of Hardy-Weinberg (Table 5). No genotypic frequencies deviated significantly from the expectations of Hardy-

TABLE 2. SEX COMPOSITION AND SL (MM) FOR ALL MORPHOTYPE SPECIMENS OF *Pseudopentaceros wheeleri* EXAMINED FOR MORPHOMETRICS AND MERISTICS.

Morphotype	n	Sex			Standard length		
		Female	Male	Undetermined	Mean	SD	Range
Lean[a]	108	33	74	1	244.8	10.58	218–276
Intermediate[a]	105	73	31	1	262.1	8.18	239–281
Fat[a]	103	53	49	1	259.8	11.34	225–280
Open ocean fat[b]	14	1	2	11	117.0	92.91	40–278
Large adult[c]	7	2	5	0	425.6	26.30	397–463
Total	337	162	161	14			

[a] Hancock Seamounts.
[b] North Pacific open ocean.
[c] Northwestern Hawaiian Islands.

Weinberg equilibrium, and data pooled over the morphotype groups failed to reveal an increase in heterozygote deficiencies (i.e., the D values, where D = the difference between number of observed heterozygotes and number of expected heterozygotes divided by number of expected heterozygotes). The principal limitations of these tests were: 1) the small number of SE-NHR fat type; and 2) that the absence of differences does not prove genetic equivalence. Nevertheless, in conjunction with the morphological data presented here, we believe the analysis of the electrophoretic character set does not indicate the presence of more than one gene pool of the pelagic armorhead.

DISCUSSION

Our morphometric results indicate that no discrete ranges in SL/BDEPTH and HL/IO separated any one morphotype from the rest; therefore, no basis exists for the species separation of North Pacific pelagic armorhead as proposed by Hardy (1983). We believe that the absence of SE-NHR fat and intermediate types the material available to Hardy accounts for his conclusions. Furthermore, no meristic or electrophoretic evidence was found to support the existence of more than one North Pacific species. We therefore conclude that there is a single, metamorphic species of pelagic armorhead in the North Pacific Ocean.

Because *P. wheeleri* and *P. pectoralis* were originally described simultaneously by Hardy (1983), we, as first revisers, follow standard nomenclatural procedures in chosing *P. wheeleri* as the valid name for the North Pacific pelagic armorhead, this binomen having page priority over *P. pectoralis*. At the same time, we argue that the high degree of morphological variation in *P. wheeleri* can be attributed to ontogeny.

Pseudopentaceros wheeleri spawns at the SE-NHR seamounts between Dec. and Feb. (Bilim et al., 1978). Well-developed ovaries were observed among Hancock Seamount lean and intermediate types collected in Nov. 1982, but those of the fat type showed little development. Nearly mature ovaries occurred in four large adult individuals collected from French Frigate Shoals in Dec. 1985–Jan. 1986. Neustonic postlarvae (10–15 mm TL) collected adjacent to the Hancock Seamounts in late Feb. 1985 resembled the open ocean fat type in coloration and relative BDEPTH (Humphreys, unpubl.). Specimens 5–40 mm SL also were collected in surface tows conducted throughout the SE-NHR region in March–April 1969 and Feb. 1976 (Borets, 1975, 1979). Egg, larval, and postlarval stages have not been reported elsewhere in the North Pacific. Juveniles have not been collected from the SE-NHR seamounts but occur in oceanic surface waters of the north and eastern North Pacific (Honma and Mizusawa, 1969; Chikuni, 1970; Borets, 1975). These juveniles resemble the adult-sized open ocean fat type. The range of life stages among open ocean fat type sharply contrasts with the presence of only adult lean, intermediate, and fat types at the SE-NHR seamounts. The SE-NHR armorhead (all morphotypes combined) also are characterized by a narrow size distribution (25–33 cm FL) that differs little between seamounts (Takahashi and Sasaki, 1977). In the NWHI, only large (≥46 cm FL) adults resembling intermediate type have been found (Tagami, unpubl.).

Of the three SE-NHR morphotypes, the lean type exhibited the greatest range in apparent physical condition. The existence of very lean

Table 3. Frequency, Mean, and 95% Confidence Limits (CL) of Meristic Characters for Morphotypes of *Pseudopentaceros wheeleri*.

Morphotype	Dorsal-fin spines					Dorsal-fin rays						Anal-fin spines					Anal-fin rays					Pectoral-fin rays				
	13	14	15	Mean	95% CL	7	8	9	10	Mean	95% CL	3	4	5	Mean	95% CL	6	7	8	Mean	95% CL	17	18	19	Mean	95% CL
Lean	13	94	1	13.89	13.83–13.95		20	81	7	8.88	8.79–8.97	1	102	3	4.02	3.98–4.06	1	60	45	7.42	7.32–7.52	34	67	7	17.75	17.64–17.86
Intermediate	16	87	1	13.86	13.79–13.93	1	18	79	6	8.87	8.77–8.97	1	103	1	4.00	3.97–4.03	4	62	39	7.33	7.23–7.43	33	66	6	17.74	17.63–17.85
Fat	14	87	2	13.88	13.81–13.95		29	69	5	8.77	8.67–8.87	1	101	1	4.00	3.97–4.03	1	78	24	7.22	7.13–7.31	34	64	5	17.72	17.61–17.83
Open ocean fat	2	12		13.86			1	11	2	9.07			14		4.00		1	7	6	7.36		7	7		17.50	
Large adult	1	5	1	14.00			1	5	2	9.00			5	2	4.29			5	2	7.29		3	4		17.57	

Morphotype	Lateral line scales																								
	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	Mean	95% CL
Lean	1		1	3	4	10	10	4	13	9	12	13	2	7	6	2	2	3	2	1		1		1	73.57	72.77–74.37
Intermediate		2	2		11	7	9	8	10	4	11	13	6	9	4	2	6			1					73.09	72.35–73.83
Fat		3	2	3	8	10	11	7	10	7	10	9	7	8	3	2	1	2							72.40	71.68–73.12
Open ocean fat		1		1		1			2		1	1	1	1		1					1				73.64	
Large adult	2			1			2			1	1														68.86	

Morphotype	Scale rows below lateral line																
	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	Mean	95% CL
Lean	1	5	2	6	9	14	17	17	13	11	2	4	2		2	43.41	42.89–43.93
Intermediate		1	5	5	12	11	12	25	5	5	10	6	3			43.63	43.12–44.14
Fat		1	3	6	5	12	11	18	22	10	4	5	3	2		43.73	43.24–43.97
Open ocean fat			1			2	3	1	2	1			1			43.73	
Large adult				1	2	1			1	2						43.00	

Morphotype	Midline scales from isthmus to pelvic-fin insertion												Upper gill rakers					
	22	23	24	25	26	27	28	29	30	31	Mean	95% CL	6	7	8	9	Mean	95% CL
Lean	2	5	11	18	24	23	14	8	2		26.19	25.86–26.52	4	58	42	4	7.43	7.31–7.55
Intermediate	4	4	18	17	20	17	17	5	2	1	25.98	25.62–26.34	7	50	43	5	7.44	7.31–7.57
Fat			3	4	3	2	1	3			26.19	25.23–27.15	5	61	36	1	7.32	7.21–7.43
Open ocean fat	1	1	3	2	3	4					25.21			8	2	1	7.36	
Large adult			1			2	4				27.14		1	4	2		7.14	

TABLE 3. CONTINUED.

Morphotype	Lower gill rakers									Total gill rakers									
	15	16	17	18	19	20	21	Mean	95% CL	22	23	24	25	26	27	28	29	Mean	95% CL
Lean		3	33	56	16			17.79	17.65–17.93	1	2	26	36	31	11	1		25.21	25.01–25.41
Intermediate		3	39	48	12	2	1	17.75	17.59–17.91		6	25	32	31	8	2	1	25.19	24.97–25.41
Fat		4	37	53	9			17.65	17.52–17.78	1	4	26	45	20	7			24.97	24.78–25.16
Open ocean fat	1	1	2	6	1			17.45		1	1	2	4	1	2			24.82	
Large adult				4	3			18.43				1	1	5				25.57	

Morphotype	Precaudal vertebrae					Caudal vertebrae					Total vertebrae				
	11	12	13	Mean	95% CL	12	13	14	Mean	95% CL	24	25	26	Mean	95% CL
Lean		73	1	12.01	11.98–12.04	5	69		12.93	12.87–12.99	4	100	1	24.97	24.93–25.01
Intermediate		85	1	12.01	11.99–12.03	4	82		12.95	12.91–12.99	4	99	1	24.97	24.93–25.01
Fat		101		12.00		4	96	1	12.97	12.93–13.01	4	97	1	24.97	24.93–25.01
Open ocean fat		3		12.00			3		13.00			3		25.00	
Large adult	1	3		11.75			3	1	13.25			4		25.00	

TABLE 4. OBSERVED ALLELE FREQUENCIES AND AVERAGE HETEROZYGOSITIES (h) AT THE MOST POLYMORPHIC LOCI FOR THREE MORPHOLOGICAL TYPES OF *Pseudopentaceros wheeleri*. (n) = Number of fish examined.

		Morphotype		
Locus	Allele	Lean	Intermediate	Fat
Adh	−100	0.725	0.644	0.659
(h = 0.434)	−200	0.265	0.351	0.318
	−250	0.010	0.005	0.000
	−30	0.000	0.000	0.023
	(n)	(100)	(97)	(22)
Ah-1	100	0.757	0.758	0.708
(h = 0.356)	90	0.208	0.216	0.292
	107	0.010	0.015	0.000
	83	0.025	0.010	0.000
	(n)	(101)	(97)	(24)
Ck-1	−100	0.828	0.831	0.886
(h = 0.260)	−50	0.172	0.169	0.114
	(n)	(93)	(89)	(22)
Est-1	100	0.832	0.861	0.833
(h = 0.230)	90	0.168	0.139	0.167
	(n)	(101)	(97)	(24)
Gpi-1	100	0.658	0.624	0.524
(h = 0.575)	141	0.168	0.165	0.262
	56	0.099	0.144	0.143
	19	0.074	0.067	0.071
	(n)	(101)	(97)	(21)
Gpi-2	100	0.985	0.964	0.977
(h = 0.050)	115	0.010	0.010	0.023
	91	0.005	0.026	0.000
	(n)	(101)	(98)	(22)
Idh-1	100	0.920	0.940	0.841
(h = 0.160)	40	0.080	0.060	0.159
	(n)	(100)	(91)	(22)
Lt	100	0.969	0.980	1.000
(h = 0.046)	78	0.005	0.010	0.000
	88	0.015	0.005	0.000
	108	0.010	0.005	0.000
	(n)	(97)	(98)	(22)
Mdh-3	100	0.970	0.964	1.000
(h = 0.058)	75	0.030	0.038	0.000
	(n)	(101)	(98)	(24)
Mpi	100	0.984	0.959	1.000
(h = 0.051)	90	0.005	0.041	0.000
	79	0.010	0.000	0.000
	(n)	(96)	(97)	(24)
Ntp	100	0.988	1.000	0.938
(h = 0.024)	120	0.012	0.000	0.063
	(n)	(81)	(70)	(16)
Pgm	100	0.535	0.449	0.604
(h = 0.583)	221	0.426	0.480	0.354
	129	0.035	0.051	0.042
	271	0.000	0.010	0.000
	0	0.005	0.010	0.000
	(n)	(101)	(98)	(24)
Sdh	100	0.909	0.941	0.979
(h = 0.138)	138	0.086	0.059	0.021
	19	0.005	0.000	0.000
	(n)	(99)	(94)	(24)

individuals, hereafter referred to as "ultra-lean" type, were reported from the Hancock Seamounts by Kuroiwa (1973), the Japan Fisheries Agency (1974), and observed in our study. The ultra-lean type are distinguishable from the lean type by their extreme emaciation, deteriorating skin, absence of visceral fat, discolored viscera, and occasional yellowish tinge. These individuals appear moribund.

Life histories have been proposed for *P. wheeleri* by Chikuni (1970) and Borets (1980). Chikuni (1970) believed that they probably inhabit the surface or near-surface layer as larvae, then undergo a vertical expansion in habitat and begin schooling as juveniles. At 25–33 cm FL, they prefer seamount summits. A preferred temperature range of 8–15 C for *P. wheeleri* affords the summits of the SE-NHR seamounts as suitable habitat and restricts *P. wheeleri* from the deeper northern Emperor Seamounts. Borets (1980) believed that open ocean adults off Japan and North America represent sterile populations formed by a small segment of the SE-NHR progeny that drift too far beyond the seamounts. Based on these earlier proposals, we now offer a life-history hypothesis that also accounts for the morphological variation.

The open ocean fat type comprises all *P. wheeleri*, from postlarvae to adult-sized individuals during their epipelagic development phase. Accumulation of fat reserves and continuous somatic growth characterize this phase, but adults remain nonreproductive. During May–Sept., open ocean fat type (25–33 cm FL) individuals recruit to the summits and upper slopes of the SE-NHR seamounts. The age of new recruits usually ranges from 18–30 mo (Uchiyama and Sampaga, unpubl.). Newly settled adults have

TABLE 5. RESULTS OF FOUR SEPARATE TESTS ON *Pseudopentaceros wheeleri* ELECTROPHORETIC DATA FOR HARDY-WEINBERG EQUILIBRIUM AT THE POLYMORPHIC LOCI FOR WHICH THE FREQUENCY OF THE COMMON ALLELE IS <0.95. Phenotypic frequencies were pooled to three classes for each locus; therefore, df = 1 for each test. The D value is the difference between number of observed heterozygotes and number of expected heterozygotes divided by number of expected heterozygotes. A negative D value indicates a heterozygote deficiency.

	Lean (n = 101)		Intermediate (n = 98)		Fat (n = 23)		Pooled (n = 222)	
Locus	χ^2	D	χ^2	D	χ^2	D	χ^2	D
Adh	0.05	−0.010	0.01	0.004	0.18	−0.020	0.09	−0.012
Ah-1	1.24	−0.094	0.52	−0.074	0.00	0.008	1.48	−0.076
Ck-1	2.68	−0.170	1.34	0.123	2.30	−0.323	0.58	−0.054
Est-1	2.31	−0.151	0.90	−0.096	0.24	−0.100	3.46	−0.125
Gpi-1	4.48*	0.117	0.01	−0.022	0.04	0.056	1.32	0.043
Idh	0.76	0.087	0.38	0.064	0.79	0.189	1.60	0.087
Pgm	1.32	0.080	0.39	0.082	0.04	−0.015	1.62	0.063
Sdh	0.99	0.094	0.36	0.062	0.01	0.021	1.20	0.072
Total	13.83	−0.047	3.91	0.143	3.60	−0.184	11.35	−0.002
P (df = 8)	0.086		0.865		0.891		0.183	

* *P* = 0.034.

already lost their mottled coloration and appear bluish gray (characteristic of SE-NHR fat type). Subsequently, coloration becomes brownish, linear growth essentially ceases, and the use of fat reserves begins, causing a decrease in relative BDEPTH and transformation to an intermediate type. The transformation to the intermediate type (particularly the change in coloration) is rapid and accounts for the low relative abundance of SE-NHR fat type during the recruitment period. Further use of fat reserves produces the lean type. As spawning season approaches, the onset of reproductive activity among intermediate and lean types is probably the most demanding energetically and may increase the conversion rate of fat reserves. Reproduction and possibly new environmental conditions associated with their new habitat may accelerate the transformation process just prior to, and during, the spawning season. Therefore, individuals recruited in May will undergo a greater degree of transformation before the start of the next spawning season than those recruited in Sept.

The morphotype composition of SE-NHR *P. wheeleri* prior to, and after, the spawning season will also be determined by the overall CF of the new recruits. A peak recruitment in May coupled with a lower average condition factor among recruits results in a predominance of the ultra-lean type after the spawning season. Peak recruitment in Sept. and a higher average CF among recruits result in an excess of intermediate and lean types after spawning. Therefore, the extent of semelparity among the spawning population is determined by arrival time and overall CF of the new recruits.

The apparent absence of new recruits <25 cm FL suggests that a minimum size is needed to insure the availability of sufficient energy reserves for reproduction. The large adult type individuals originate from open ocean fat type that "stray" south from the main open ocean population, undergo a longer epipelagic phase, and eventually settle and reproduce around the NWHI. Most of these individuals tend to be 4–5 yr olds as compared to the 2–3 yr olds captured at the Hancock Seamounts (Uchiyama and Sampaga, unpubl.). Implicit in this hypothesis are assumptions that morphotype transformation is a one-way process, transformed individuals remain at a particular seamount until death, and the SE-NHR seamounts offer the most favorable habitat and means for congregating open ocean fat type from throughout the North Pacific for subsequent reproduction.

A life history involving an extended epipelagic phase followed by a change in habitat preference and morphology is rare but not unique in fishes. A similar life history mode is exemplified by the freshwater eel *Anguilla* in the North Atlantic Ocean (Williams and Koehn, 1984). Although various aspects of the *Anguilla* life history parallel those proposed for *P. wheeleri*, considerable research is needed to test our hypothesis. Currently, our work on this hypothesis focuses on the determination and significance of the physiological changes throughout transformation and on a technique to assess the seamount residence time of transformed individuals.

Material Examined

BPBM 25156, North Pacific Ocean, 45°41′N, 165°05′W (2); BPBM 15757, North Pacific Ocean, 44°39′N, 174°48′W (2); SWFC uncat., North Pacific Ocean, 38°30′N, 175°03′W (6); SWFC uncat., North Pacific Ocean (1); SWFC uncat., North Pacific Ocean, 45°30′N, 155°00′W (2); SWFC uncat., North Pacific Ocean, 45°26′N, 154°58′W (1); BPBM 27853, NWHI, Kure Atoll (1); SWFC uncat., NWHI, Lavsan Island (1); SWFC uncat., NWHI, French Frigate Shoals (5).

Acknowledgments

We thank W. Barnett and the officers and crew of the NOAA ship TOWNSEND CROMWELL for assistance with field collections and P. Aebersold for assistance with the electrophoresis. G. Boehlert, G. Hardy, D. Johnson, and R. Rosenblatt reviewed the manuscript and offered helpful suggestions.

Literature Cited

Allendorf, F. W., N. Mitchell, N. Ryman and G. Stahl. 1977. Isozyme loci in brown trout (*Salmo trutta* L.): detection and interpretation from population data. Hereditas 86:179–190.

Bilim, L. A., L. A. Borets and L. K. Platoshina. 1978. Characteristics of ovogenesis and spawning of the boarfish in the region of the Hawaiian Islands. Izv. Pac. Ocean Sci. Res. Inst. Fish. Oceanogr. (TINRO) Vladivostok 102:51–57. Translated from Russian by W. G. Van Campen. 1986. Trans. No. 106. (Available Southwest Fisheries Center, NMFS, NOAA, Honolulu, Hawaii.)

Borets, L. A. 1975. Some results of studies on the biology of the boarfish (*Pentaceros richardsoni* Smith). Invest. Biol. Fishes Fish. Oceanogr. (TINRO) Vladivostok 6:82–90. Translated from Russian by W. G. Van Campen. 1984. Trans. No. 97. (Available *Ibid.*)

———. 1979. The population structure of the boarfish, *Pentaceros richardsoni*, from the Emperor Seamounts and the Hawaiian Ridge. J. Ichthyol. 19(3): 15–20.

———. 1980. The distribution and structure of the range of the boarfish *Pentaceros richardsoni*. *Ibid.* 20(3):141–143.

Boyer, S. H., D. C. Fainer and E. J. Watson-Williams. 1963. Lactate dehydrogenase variant from human blood: evidence for molecular subunits. Science 141: 642–643.

Chikuni, S. 1970. The "phantom fish," "kusakari tsubodai"—an outline. Enyo (Far Seas) Fish. Res. Lab. News 3:1–4. Translated from Japanese by J. H. Shohara (nd). (Available NMFS, NOAA, Southwest Region, Terminal Island, California.)

Clayton, J. W., and D. N. Tretiak. 1972. Amine-citrate buffers for pH control in starch gel electrophoresis. J. Fish. Res. Bd. Can. 29:1169–1172.

Follett, W. I., and L. J. Dempster. 1963. Relationships of the percoid fish *Pentaceros richardsoni* Smith, with description of a specimen from the coast of California. Proc. Calif. Acad. Sci. 32:315–338.

Hardy, G. S. 1983. A revision of the fishes of the family Pentacerotidiae (Perciformes). N. Zeal. J. Zool. 10:177–220.

Honma, Y., and R. Mizusawa. 1969. A record of the young of boar fish, *Pseudopentaceros richardsoni*, from the North Pacific. Jap. J. Ichthyol. 15(3):134–136. Translated from Japanese with English summary by T. Otsu. 1983. (Available Southwest Fisheries Center, NMFS, NOAA, Honolulu, Hawaii.)

Hubbs, C. L., and K. F. Lagler. 1958. Fishes of the Great Lakes region. University of Michigan Press, Ann Arbor, Michigan.

Japan Fisheries Agency. 1974. Survey of the North Pacific seamounts (Kita Taiheiyō kaizan chōsa). Report of *Kaiyo Maru* survey cruises, 1972 season. Jap. Fish. Agency. Translated from Japanese by T. Otsu. 1981. Trans. No. 54. (Available Southwest Fisheries Center, NMFS, NOAA, Honolulu, Hawaii.)

Kotlyar, A. N. 1982. First finding of *Parazen pacificus* Kamohara (Zeidae) and *Pentaceros richardsoni* (Pentacerotidae) in the Indian Ocean. Bull. Mosk. O-Va. Ispyt. Prir. Otd. Biol. 87(3):34–36 [In Russian].

Kuroiwa, M. 1973. Research by trawl fishery for commercialization of the fishing grounds by Japan Marine Fishery Resource Research Center . . . Outline of trawl fishery investigation for commercialization in the central North Pacific Ocean—I. Bull. Jpn. Soc. Fish. Oceanogr. 23:42–47. Translated from Japanese by T. Otsu. 1984. Trans. No. 95. (Available Southwest Fisheries Center, NMFS, NOAA, Honolulu, Hawaii.)

Ridgway, G. J., S. W. Sherburne and R. D. Lewis. 1970. Polymorphism in the esterases of Atlantic herring. Trans. Amer. Fish. Soc. 99:147–151.

Sasaki, T. 1974. The pelagic armorhead, *Pentaceros richardsoni* Smith, in the North Pacific (Kita Taiheiyō no kusakari tsubodai). Bull. Jpn. Soc. Fish. Oceanogr. 24:156–165. Translated from Japanese by T. Otsu. 1977. Trans. No. 16. (Available Southwest Fisheries Center, NMFS, NOAA, Honolulu, Hawaii.)

Shaw, C. R., and R. Prasad. 1970. Starch gel electrophoresis of enzymes—a compilation of recipes. Biochem. Genet. 4:297–320.

Takahashi, Y., and T. Sasaki. 1977. Trawl fishery in the central North Pacific seamounts (Kita Taiheiyō chubu kaizan ni okeru torōru gyogyō). Hokuyo soko-uo gyogyō—Shiryo (3) (Northern waters groundfish fishery—Data [3]). Division of Northern Waters Groundfish Resources, Far Seas Fish. Res. Lab. Translated from Japanese by T. Otsu.

1977. Trans. No. 22. (Available Southwest Fisheries Center, NMFS, NOAA, Honolulu, Hawaii.)

Turner, B. J., and D. J. Grosse. 1980. Trophic differentiation in *Ilyodon*, a genus of stream-dwelling goodeid fishes: speciation versus ecological polymorphism. Evolution 34(2):259–270.

Utter, F. M., P. A. Aebersold and G. A. Winans. 1987. Interpreting genetic variation detected by electrophoresis, p. 21–45. *In:* Population genetics and fisheries management. N. Ryman and F. Utter (eds.). University of Washington Press, Seattle, Washington.

Williams, G. C., and R. K. Koehn. 1984. Population genetics of North Atlantic catadromous eels (*Anguilla*), p. 529–560. *In:* Evolutionary genetics of fishes. B. J. Turner (ed.). Plenum Press, New York, New York.

Winans, G. A., and L. L. Jones. 1988. Electrophoretic variability in Dall's porpoise (*Phocoenoides dalli*) in the North Pacific Ocean and Bering Sea. J. Mammal. 69:14–21.

Zar, J. H. 1984. Biostatistical analysis. 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

(RLH, DTT) Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, Hawaii 96822 and (GAW) Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, Washington 98112. Accepted 26 Feb. 1988.

8931

FECUNDITY AND OTHER ASPECTS OF THE REPRODUCTION OF SABLEFISH, *ANOPLOPOMA FIMBRIA*, IN CENTRAL CALIFORNIA WATERS

J. ROE HUNTER, BEVERLY J. MACEWICZ, AND CAROL A. KIMBRELL
National Marine Fisheries Service
Southwest Fisheries Center
P.O. Box 271
La Jolla, California 92038

ABSTRACT

Along the central California coast from Point Conception to Monterey Bay, sablefish specimens were taken in research trawls, in traps, and from the fishery. Sablefish in spawning condition occurred in October through early February. Fifty percent of the females 60 cm long were sexually mature. Most of the females with active ovaries were taken in the oxygen minimum zone; 96% of the reproductively active females occurred at depths of 800 m or deeper. The mean length of males and females taken in trawls increased with depth.

Five lines of evidence indicated that the standing stock of advanced yolked oocytes was equivalent to the total potential annual fecundity; in other words, fecundity is determinate in sablefish. The potential annual fecundity of a 2.5-kg sablefish was 107 oocytes per gram female weight; the batch fecundity averaged 24 hydrated oocytes per gram female weight for the last spawn, and 41 for earlier spawnings. Thus sablefish would have to spawn about three times to fully use their potential annual fecundity.

RESUMEN

Varios especímenes de pez sable fueron capturados en arrastres de investigación, con trampas y por la pesquería a lo largo de la costa de California, desde Punta Concepción hasta la bahía de Monterey. Desde el mes de octubre hasta los comienzos de febrero se observaron especímenes en condiciones de desove. El 50% de las hembras de 60 cm de longitud se encontraban sexualmente maduras. La mayoría de las hembras con ovarios activos provinieron de la zona de mínimo oxígeno; el 96% de las hembras reproductoras ocurrió a profundidades iguales o mayores a los 800 metros. La longitud promedio de los machos y las hembras recolectados en los arrastres aumentó proporcionalmente con la profundidad de captura.

La evidencia demostró que el stock de ovocitos vitelinos en estadíos avanzados fue equivalente a la fecundidad total potencial anual; en otras palabras, la fecundidad en el pez sable está determinada. La fecundidad potencial anual de un pez de 2.5 kg de peso fue de 107 ovocitos por gramo de hembra. La fecundidad parcial promedió 24 ovocitos hidratados por gramo de hembra para el último desove y 41 ovocitos para los desoves anteriores. De esta manera, el pez sable debiera desovar 3 veces por año para hacer uso completo de su fecundidad potencial.

INTRODUCTION

The objective of this study was to estimate fecundity, length at first maturity, bathymetric distribution, and frequency of spawning for sablefish, *Anoplopoma fimbria*, from central California, and to identify the spawning period. Sablefish occur along the northern rim of the Pacific Ocean from the southern tip of Baja California to the north-central Bering Sea and from there to central Honshu, Japan. Most of the U.S. catch is taken between southeastern Alaska and central California (MBC 1987).

We use our analysis of sablefish fecundity to evaluate the assumption of determinate fecundity. In fishes with determinate fecundity, the standing stock of advanced oocytes before spawning is equivalent to the total potential fecundity for the year. In many fishes (anchovy, sardine, mackerel, and others) fecundity is indeterminate (Hunter and Macewicz 1985a; Hunter et al. 1985); the standing stock of advanced oocytes is not equivalent to the total potential fecundity because unyolked oocytes are continuously matured and spawned during the reproductive season. Validation of the assumption of determinate fecundity is important because if determinate fecundity is wrongly assumed, total fecundity estimates are meaningless.

Some reports on sablefish reproduction exist: Mason et al. (1983) thoroughly studied fecundity (standing stock of advanced oocytes), identified the peak spawning period, and determined age and size at maturity of Canadian sablefish; Phillips and Imamura (1954) give some incidental values of standing stock of advanced oocytes for a few fish from California; Cailliet et al. (1988) estimated seasonality of reproduction, and report on the relation between bathymetry, size, and sexual maturity for

[Manuscript received February 1, 1989.]

fish from Monterey Bay, California; Fujiwara and Hankin (1988) report similar information for northern California; and Norris et al. (1987) estimated the seasonality of reproduction for fish from the Oregon and Washington coasts. No sablefish study has considered the frequency of spawning or evaluated the assumption of determinate fecundity.

METHODS

Collections and Shipboard Measurements

Sablefish were collected along the central California coast (Point Conception to San Francisco Bay) during two research trawl surveys (January–February 1987; February–April 1988), during a trap survey conducted by the NWAFC (October 1986), and from the fishery by the California Department of Fish and Game (October 1986–February 1987). Research trawls were about one hour long in 1987, and were taken at fixed and repeated stations at seven depths (100–700 fath., 183–1280 m) in 1987. In 1988, random trawl samples were taken within three depth strata (30–249 fath., 55–455 m; 250–549 fath., 457–1004 m; 550–699 fath., 1006–1278 m) with tow durations of 0.5 hr in the first stratum and 1.0 hr in the middle and the deep strata. The trawl used was a 400-mesh Eastern with a mouth width of about 15 m, and height about 1.5 m (Wathne 1977).

In the 1986 trap survey, the females collected for fecundity were weighed and measured (FL, fork length) at the time of capture. In both trawl surveys (1987 and 1988) the total catch of sablefish was weighed; each fish was sexed and measured (FL); and a wet weight of most of the females was taken. The data were used to describe the bathymetric distribution of sablefish. We used the trawl catch of sablefish (kg/hr) to relate abundance to depth, but because the trawl extended only 1.5 m from the bottom, biomass is probably greatly underestimated by the catch; the average catch altitude for sablefish caught on setlines by Sullivan (1982) was 12 m off the bottom. In the 1987 survey, bottom temperatures and oxygen concentration were measured over the depth range of the survey (100–700 fath., 183–1280 m).

Reproductive measurements were made only during the 1986 and 1987 surveys. Data from the 1988 survey were used only to define the bathymetric distribution of sablefish. In 1988, ovaries were classed on shipboard into three types: hydrated (ovaries containing translucent hydrated yolked oocytes); active (ovaries containing yolked oocytes); and inactive (ovaries containing neither hydrated nor other yolked oocytes). The inactive class includes stages designated in other classification schemes as "spent," "immature," and various "developing" stages. In 1986–87 a five-class table was used, but we believe no useful purpose was served by attempting to make such distinctions, which in some cases are highly subjective. Although "spent" ovaries can be identified with reasonable accuracy immediately after a spawning, we did not use this stage because it is an ephemeral stage of unknown duration. An ovary classified as "spent" transforms into an inactive or active state depending on whether the female has completed all spawnings or will spawn again. Ovaries from females used in fecundity estimates were frozen or preserved in 10% neutral buffered Formalin and then weighed in the laboratory.

The length at first maturity was estimated by calculating the fraction of the ovaries that were active per length class for fish taken early in the spawning season (October 1986).

The fraction of females with hydrated ovaries taken in research trawls (1987 and 1988) was used to estimate the time of day that sablefish spawn.

Total Fecundity

We measured the total fecundity of 45 females captured in sablefish traps (October 20–27, 1986), and of 41 females taken in research trawls (January 17–February 14, 1987). Total fecundity (F_T) is defined as the total number of advanced yolked oocytes in the ovary, including all hydrated oocytes.

We estimated total fecundity gravimetrically. Using this method, fecundity (F_T) is the product of the gonad weight (G) and oocyte density (C). Oocyte density is the number of oocytes, within a specified diameter range, per gram of ovarian tissue, and is determined by counting the number of advanced oocytes in a weighed sample of ovarian tissue. We looked for differences in oocyte density between the right and left ovary and found none. We then removed two tissue samples from the right ovary, and counted all the advanced yolked oocytes in both samples. In one of the samples we also measured the diameters of 30 randomly selected advanced yolked oocytes. Advanced oocytes were identified, counted, and measured using a digitizer linked by a video camera system to a dissection microscope.

Measuring the diameter of the advanced oocytes served several functions. It provided a criterion for selecting ovaries that had matured enough to accurately estimate the density of advanced oocytes (see next section). Diameter was also used to determine seasonal changes in maturity of the advanced group of oocytes. Finally, diameter provided an alternate method for estimating oocyte density. Oocyte density (C) can be roughly estimated from the mean diameter (D) of oocytes, because the weight of the advanced oocytes is proportional to their volume (assuming a spherical form and a specific gravity of 1). Hence,

$$C = K \frac{1}{\frac{1}{6}\pi D^3}$$

where $\frac{1}{6}\pi D^3$ is the volume of a sphere, and D is mm/10.

The coefficient of proportionality K was estimated for the October and January–February collections to determine if the density of advanced oocytes in the ovarian tissue changed over the spawning season. We did not measure the diameter of hydrated oocytes, nor did we use data from hydrated ovaries to estimate K.

Identification of the Advanced Stock of Oocytes

As a sablefish ovary matures, the standing stock of advanced yolked oocytes, believed to constitute the total fecundity for the season, gradually separates from the stock of smaller immature oocytes. When sufficiently mature, the standing stock is easily identified because it is separated from the immature oocytes by a gap in the oocyte size-frequency distribution where no or few oocytes occur (figures 1C and 1D; and illustrations of Mason 1984). Estimates of the standing stock can be biased in ovaries in which complete separation has not occurred (figures 1A and 1B). Thus for our fecundity estimates we wished to select ovaries in which the advanced oocytes were well separated from the less-advanced oocytes.

The apparent density of yolk within oocytes viewed on the video screen was used to discriminate between developmental stages of yolked oocytes. Four developmental stages were defined: stage 0, no yolk granules present (primary oocytes), oocyte diameter greater than about 0.1 mm; stage 1, initial layer of yolk along the periphery of the oocyte, appearing as a narrow band not extending over 20% of the distance between the nucleus and the zona pellucida; stage 2, layer of yolk extending from periphery to the nucleus, but nucleus is clearly visible; stage 3, yolk sufficiently dense that the nucleus is indistinct or occluded (advanced oocytes).

Examination of six ovaries indicated that when the mean size of the oocytes in stage 3 (advanced yolked oocytes) was greater than 0.7 mm, the separation of the advanced mode of oocytes from those in stages 1 and 2 was nearly complete. Thus, in our routine fecundity measurements we counted and measured only advanced yolked oocytes as defined above. If the mean of such oocytes was greater than 0.7 mm we included the data, but if the mean diameter ≤ 0.7 mm, the ovary was rejected because it was not sufficiently mature for an accurate estimate of the standing stock of advanced yolked oocytes.

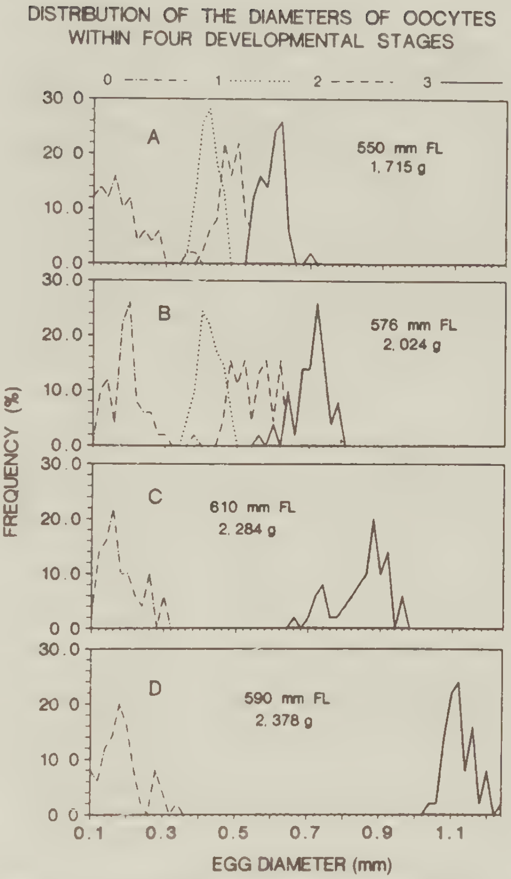


Figure 1. The frequency distribution of the diameter of oocytes within four maturity stages based on apparent yolk concentration. Each panel presents data for one female. Stages range from 0 (no yolk) to stage 3, the most advanced stage (used to estimate fecundity). *A* and *B*, sablefish ovaries in which separation of advanced standing stock (stage 3) is incomplete; *C* and *D*, ovaries where advanced oocytes are completely separated from other yolked oocytes.

Batch Fecundity

The number of hydrated oocytes in an ovary is equivalent to the batch fecundity (F_B) — the number of oocytes released during one spawning. Owing to their large diameter (about 2 mm) and translucent appearance, hydrated oocytes are easily identified. Batch fecundity was estimated for 17 females taken in the 1987 research trawl survey by counting the number of hydrated oocytes in two tissue samples per ovary. We also estimated the number of nonhydrated advanced oocytes present in the same ovary using the procedure described for estimating total fecundity. A sample of 17 ovaries was too small to determine the relation between fish weight (W, always calculated as ovary-free female weight) and batch fecundity; thus batch fecundity was expressed as relative batch fecundity (F_B/W) [batch fecundity/ovary free female weight]. Total fecundity (F_T) for females with hydrated ovaries was the sum of the hydrated and advanced yolked oocytes.

Histological Analysis

Fresh ovaries from the 1987 research trawl survey were preserved in 10% neutral buffered Formalin and embedded in Paraplast. Histological sections were cut at 5–6 μm and stained with Harris hematoxylin followed by eosin counterstain (H&E). We did not histologically examine ovaries from the October 1986 survey because most of the fish had been frozen before being preserved in Formalin. Consequently, they were unsuitable for detailed histological analysis. Ovaries of sablefish taken in 1988 were not preserved.

Each ovary was classified histologically in the manner developed for northern anchovy (*Engraulis mordax*) by Hunter and Goldberg (1980), and Hunter and Macewicz (1980, 1985a,b), with a few modifications appropriate for sablefish ovarian structure. In the ovary we identified the presence or absence of oocytes in the first vitellogenic stages; advanced yolked oocytes; migratory nucleus stage oocytes (precursor to hydration); hydrated oocytes; postovulatory follicles; and three stages of atretic oocytes. The rate at which postovulatory follicles are resorbed in sablefish is unknown. Thus no ages were assigned to postovulatory follicles. Spent ovaries usually contained two groups of postovulatory follicles of differing deterioration, indicating two past spawnings. The oldest group of postovulatory follicles had to be at least 48 hr old; we suspect they were older because of their small size and extent of resorption.

RESULTS

Seasonal and Daily Timing of Spawning

The percentage of all females with reproductively active ovaries declined between October and February (figure 2). Similarly, ovary weight of Monterey sablefish declined markedly between November–December and January–February (Cailliet et al. 1988). These data indicate that the peak spawning period for sablefish in central California probably occurs sometime between October and February.

On a daily basis, peak spawning may occur between 1300 and 1600 hours. The proportion of females with hydrated ovaries was highest (24%) between 0900 and 1200 hrs and was low (2%) during the rest of the day, indicating that most females may have spawned by 1300 (table 1). No females with hydrated oocytes were taken at night (1700–0400), indicating that the hydrated oocyte stage may be shorter than 24 hours and that, collectively,

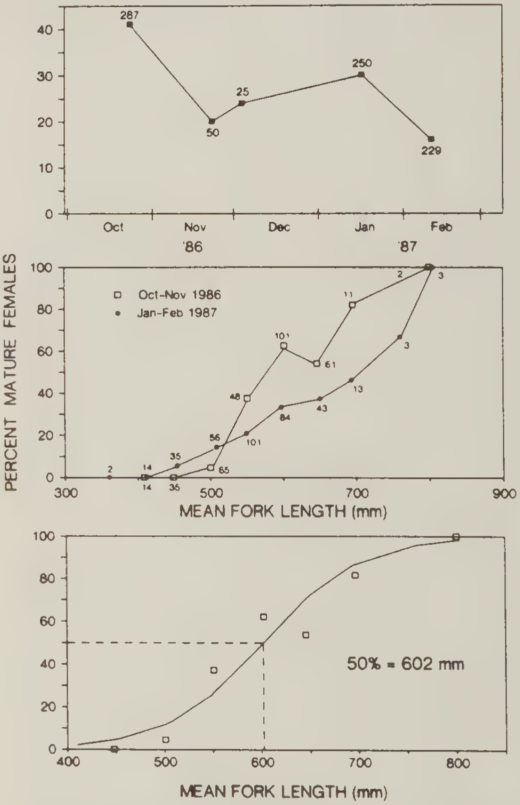


Figure 2. Fraction of sablefish ovaries that were active (yolked oocytes present) during 1986–87 spawning season as a function of collection date (*upper panel*) and fork length (*middle panel*), where squares are sablefish taken in October–November 1986 trap survey, and circles are January–February 1987 trawl survey; fraction active was calculated by 50-mm length classes; numbers are the number of fish per length class. *Lower panel*, fraction of females mature within each 50-mm length class; estimated length at 50% maturity = 602 mm.

TABLE 1
Percentage of Female Sablefish with Ovaries Containing Hydrated Oocytes

Time of capture	Total N	Percent hydrated
0030–0429	20	0
0430–0829	50	2.0
0830–1229	67	23.9
1230–1629	111	1.8
1630–2029	30	0
2030–0029	75	0
Entire day	353	5.4

Data from January–February 1987 survey.

the processes of hydration, ovulation, and spawning may require less than 24 hours to complete.

Length, Maturity, and Bathymetry

The percent maturity of sablefish females (P) as a function of fork length was estimated using the logistic regression

$$P = \frac{e^{a+bx}}{1 + e^{a+bx}}$$

where x = forklength in mm; $a = -11.978$, SE(a) = 1.439, $t(a) = -8.322$; $b = 0.020$, SE(b) = 0.00244, $t(b) = 8.177$; and DF = 335. In October the percentage of females with active ovaries increased with length; about 50% of females were reproductively active at 60 cm FL (figure 2). Misclassification of mature females as immature was unlikely because October was early in the spawning season. Our estimate of female length at first maturity (60 cm FL) was similar to that for females from British Columbia, where values ranged from 58 to 62 cm FL (Mason et al. 1983), and to that for females from northern California (56 cm; Fujiwara and Hankin 1988).

The mean length of males and females taken in trawls increased with depth, and the rate of change of length with depth was about the same in the two surveys (figure 3). At most depths, the average female and male sablefish taken in traps were longer than those taken in trawls. The mean length of fish taken in traps increased more slowly with depth than it did for those taken in the trawl. The lengths of fish taken by the two gears were about the same at depths of 500 fath. (914 m) or more, presumably because small sablefish do not occur at such depths.

Of the 87 female sablefish with active ovaries taken in January–February 1987, 96% were taken at depths of 450 fath. (823 m) or greater; most of the active females (75%) were taken between 550 and 650 fath. (1006 and 1189 m). Thus in central California, the principal spawning habitat of sablefish seems to be the continental slope at depths of 450 fath. (823 m) or greater. How far down the slope reproductively active sablefish occur is unknown. The mean length of sablefish increased with trawling depth up to the maximum depth of our trawl collections (700 fath., 1280 m), and nearly all of the females taken at 700 fath. (1280 m) were reproductively active. Although reproductively active sablefish probably occur at depths greater than 700 fath. (1280 m), their abundance may be low. The catch rates of sablefish in 1987 and 1988 reached a maximum at 500 fath. (914 m) and declined at greater depths (figure 4). The spawning habitat of sablefish in central California is characterized by low oxygen concentrations as well as low temperature (figure 5).

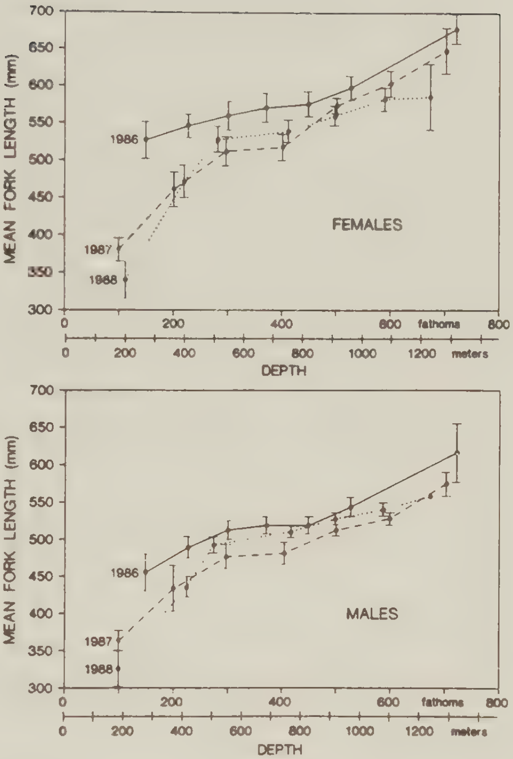


Figure 3. *Upper panel*, mean fork length (± 2 × standard error of mean) of female sablefish for 100-fath. (183-m) depth classes: *solid line*, 1986 October–November trap survey; *dashed line*, 1987 January–February trawl survey; *dotted line*, 1988 February–April trawl survey. *Lower panel*, mean fork length of males for the same surveys

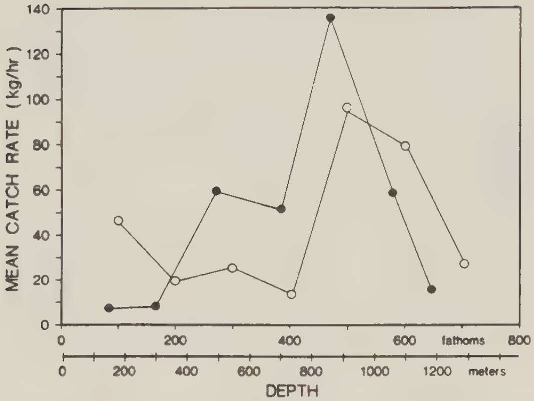


Figure 4. Catch rate of sablefish taken in 400-mesh Eastern trawl at 100-fath. (183-m) depth classes: *open circles*, 1987 survey; *solid circles*, 1988 survey.

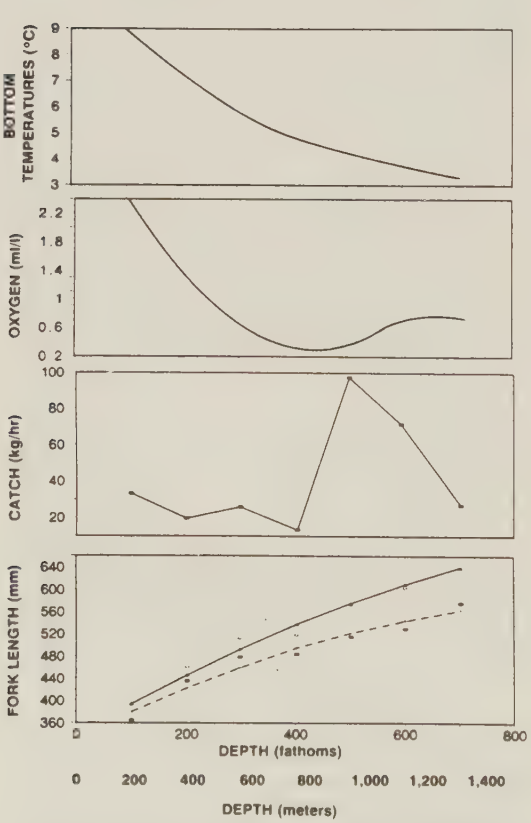


Figure 5. Relation between depth and bottom temperature, bottom oxygen concentration, sablefish catch, and fork length for 1987 survey.

Total Fecundity

The total number of advanced oocytes in the ovaries (F_T) of sablefish captured in October 1986 increased linearly with female weight (W in grams),

$$F_T = -45{,}223 + 125.1\,W,$$

where $r^2 = 0.50$; figure 6, upper, and table 2. According to this equation the total potential relative fecundity (F_T/W) of the sablefish taken in October ranged from 100 oocytes/g female weight for a 1.8-kg female, to 107 for a 2.5-kg fish. The relation between female fork length (L) and fecundity (F_T) was

$$F_T = 2.145 \times 10^{-5}\,L^{3.616}$$

where $r^2 = 0.40$.

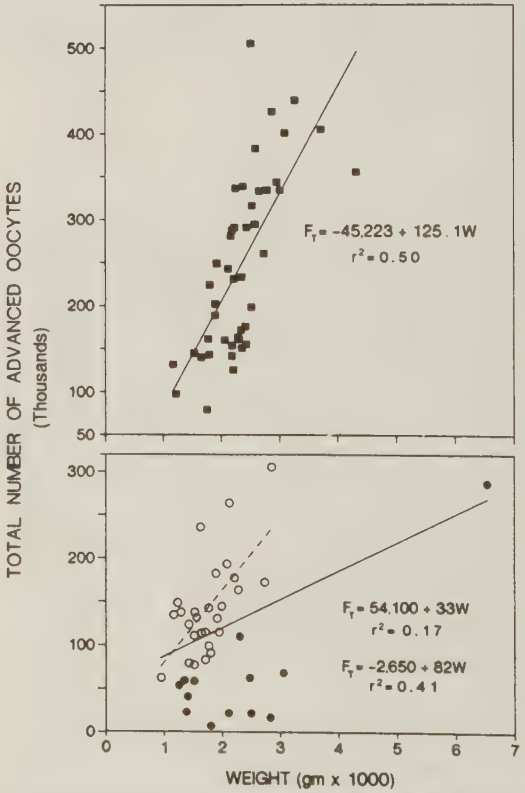


Figure 6. *Upper panel*, number of advanced oocytes in sablefish ovaries in October 1986 as a function of ovary-free female weight (N = 45). *Lower panel*, standing stock of advanced oocytes in January–February 1987 as a function of ovary-free female weight: *open circles*, no postovulatory follicles present in ovary; *solid circles*, postovulatory follicles present in ovary. *Solid line*, regression for all data (N = 41); *dashed line*, regression where ovaries with postovulatory follicles are omitted (N = 28).

TABLE 2

Standing Stock of Oocytes in Sablefish Ovaries in Order of Female Weight (Ovary-Free) Within a Survey Period

October 20 to 28, 1986

Female Wet weight (g)	Female Fork length (mm)	Female Ovary weight (g)	Standing stock of advanced oocytes (thousands)
1165	500	110	132
1218	510	49	97
1535	560	125	146
1654	540	72	140
1686	550	29	51
1752	560	93	80
1766	560	80	161
1797	550	63	143
1797	580	184	224
1891	570	122	189
1922	570	128	249
~~1988~~ [illegible]	630	202	505
2062	570	99	160
2118	590	122	243
2164	590	141	281
2182	590	112	154
2183	620	97	141
2184	610	100	288
2206	590	123	126
2207	600	178	232
2221	610	129	291
2241	580	149	336
2290	610	126	163
2312	620	159	161
2330	600	126	171
2345	590	145	232
2351	590	164	151
2362	600	65	270
2375	600	111	339
2414	620	171	176
2434	630	156	155
2440	610	121	291
2465	620	58	234
2472	610	65	388
2519	650	96	199
2534	620	107	316
2579	630	91	295
2595	610	251	382
2660	620	106	333
2728	620	242	261
2793	640	264	335
2878	640	124	426
~~2888~~ 1888	560	132	201
2953	640	127	344
3015	670	224	334
3096	670	189	401
3275	650	145	439
3394	680	136	556
3730	690	370	405
4328	720	409	356

January 16 to February 13, 1987

Female Wet weight (g)	Female Fork length (mm)	Female Ovary weight (g)	Thousands of advanced oocytes Non-hydrated	Thousands of advanced oocytes Hydrated	Thousands of advanced oocytes Total	Post-ovulatory follicles + = present − = absent
944	474	86	62	0	62	−
1173	528	133	136	0	136	−
1228	500	172	149	0	149	−
1262	515	235	0	54	54	+
1300	520	136	139	0	139	−
1355	502	281	1	59	60	+
1394	538	130	0	23	23	+
1418	552	194	0	41	41	+
1434	522	148	124	0	124	−
1441	530	104	80	0	80	−
1515	540	109	78	0	78	−
1525	557	125	112	0	112	−
1529	548	237	6	53	59	+
1543	550	169	138	0	138	−
1568	540	194	132	0	132	−
1645	632	791	103	134	237	−
1656	540	169	114	0	114	−
1698	547	171	126	0	126	−
1722	572	147	21	63	84	−
1729	545	355	64	51	115	−
1760	524	245	143	0	143	−
1779	545	291	14	86	100	−
1799	577	109	91	0	91	−
1807	595	77	6	0	6	+
1892	550	238	182	0	182	−
1920	560	215	131	0	131	−
1958	595	134	116	0	116	−
2003	605	423	74	71	145	−
2094	590	268	194	0	194	−
2107	610	153	0	22	22	+
2143	597	351	264	0	264	−
2215	590	163	178	0	178	−
2291	594	239	164	0	164	−
2309	620	391	28	82	110	+
2470	630	315	2	62	63	+
2501	636	44	22	0	22	+
2744	582	296	173	0	173	−
2838	625	122	0	17	17	+
2866	660	564	207	99	306	−
3058	665	326	0	69	69	+
6543	818	938	31	255	286	+

By January–February 1987, the standing stock of advanced oocytes had declined to about 60% of oocyte stock observed in October 1986, and was only weakly correlated with female weight:

$$F_T = 54077 + 32.8\ W,$$

$r^2 = 0.17$, (figure 6, lower). Statistical documentation for this seasonal decline in oocyte standing stock is provided by multiple regression of fecundity on elapsed time and female weight:

$$F_T = 95{,}202 - 1150\ T + 5.71\ W,$$

where T is elapsed time from October 20, and $R^2 = 0.50$. Relative fecundity (F_T/W) declined from 105 oocytes/g (SD = 36.0, N = 45) in October to 64 oocytes/g (SD = 33.9, N = 41) in January–February. A t test showed that the means were significantly different ($p < 0.05$, t = 5.41, DF = 83). This seasonal decline in the standing stock of advanced oocytes indicates that some of the females had spawned part of their advanced stock of oocytes, and these oocytes were not replaced. Therefore determinate fecundity is indicated.

The weak relation between fecundity and fish weight in January–February ($r^2 = 0.17$) was probably caused by variation in the number of spawnings completed by each female. That females with postovulatory follicles (solid circles, figure 6, lower) had the lowest fecundity for a given weight supports this conclusion. The relative fecundity of females without postovulatory follicles was 81 oocytes/g (SD = 24, N = 28), whereas that for fish with postovulatory follicles was only 26 oocytes/g (SD = 15, N = 13). Thus, spawning has reduced the standing stock of advanced oocytes and consequently supports the assumption of determinate fecundity. The relation between fecundity and female weight for January–February is much stronger if females with postovulatory follicles are excluded:

$$F_T = 82.5\ W - 2652,$$

$r^2 = 0.41$ (figure 6, dashed line). This indicates that the high variability in the January–February 1987 data was caused by spawning. The slope of the regression of fecundity on weight for January–February 1987 is lower than the one for October 1986 even when fish with postovulatory follicles are excluded. Thus spawning probably occurred in females in which no postovulatory follicles were detected. Presumably, enough time had elapsed before capture for the postovulatory follicles to be resorbed in these fish.

Batch Fecundity and Spawning Frequency

The mean relative batch fecundity (based on counts of hydrated oocytes) was higher when many advanced yolked oocytes occurred with the hydrated batch than when few or none occurred. Thus the size of the last spawning batch was lower than that of earlier batches, and the number of oocytes in the last spawn averaged 24 oocytes/g, whereas the other spawnings averaged 41 oocytes/g (table 3). A t test showed significant difference in the means ($p < 0.05$, t = 2.348, DF = 15).

TABLE 3

Relative Fecundity (Number of Advanced Yolked Oocytes per Gram Ovary-Free Female Weight) of 17 Sablefish Females with Hydrated Oocytes

Potential spawnings ≥ 2			Potential spawnings = 1		
Not hydrated[a]	Hydrated	Total	Not hydrated[b]	Hydrated	Total
72	34	106	0.64	44	45
62	81	143	0.64	25	26
37	35	72	0.09	9.8	10
37	29	66	0.07	43	43
12	36	48	0	29	29
12	36	48	0	22	22
7.6	48	56	0	16	16
4.8	39	44	0	6.0	6
3.9	34	38			
Mean batch fecundity[c]	41.3			24.3	
SD	15.7			14.0	

[a] Mean diameter = 1.44, SD = 0.059, and range 1.31–1.52.
[b] Mean diameter = 1.46, SD = 0.015, and range 1.45–1.48.
[c] Calculated from the number of hydrated oocytes

Females separated into two classes: those likely to spawn two or more batches because, in addition to the hydrated batch, substantial numbers of advanced oocytes exist in the ovary; and those in which the hydrated oocytes may be the last spawning batch because, other than the hydrated batch, few or no advanced oocytes exist in the ovary.

The mean weight of the 17 females with hydrated oocytes was 2237 g, (SD = 1245). According to our fecundity equation for fish taken early in the season (October), a fish of this weight would have a standing stock of 234,836 advanced oocytes or about 105 oocytes/g female weight. This female would have to spawn three times to use this standing stock of oocytes, assuming that the number of advanced oocytes in the last batch is 24 and the other spawnings are 41 oocytes/g female weight. In other words, division of our estimates of relative batch size into what we believe to be the initial standing stock of oocytes indicates that the average female sablefish spawns about three times per season. We assumed that if the remaining advanced oocytes were fewer than one oocyte/g, the oocytes would not be spawned and would be resorbed. The smallest hydrated batch we observed was 6 oocytes/g.

Oocyte Diameter

The mean diameter of the advanced oocytes (excluding hydrated oocytes) increased from 1.0 mm (SD = 0.17, N = 50) in October 1986 to 1.34 mm (SD = 0.15, N = 37) in January–February. A t test showed that the means differed significantly ($p < 0.05$, $t = -10.04$, DF = 81). This observation supports the assumption of determinate fecundity, because an increase in average diameter of the advanced oocytes would not be likely if new, smaller oocytes were recruited into the advanced

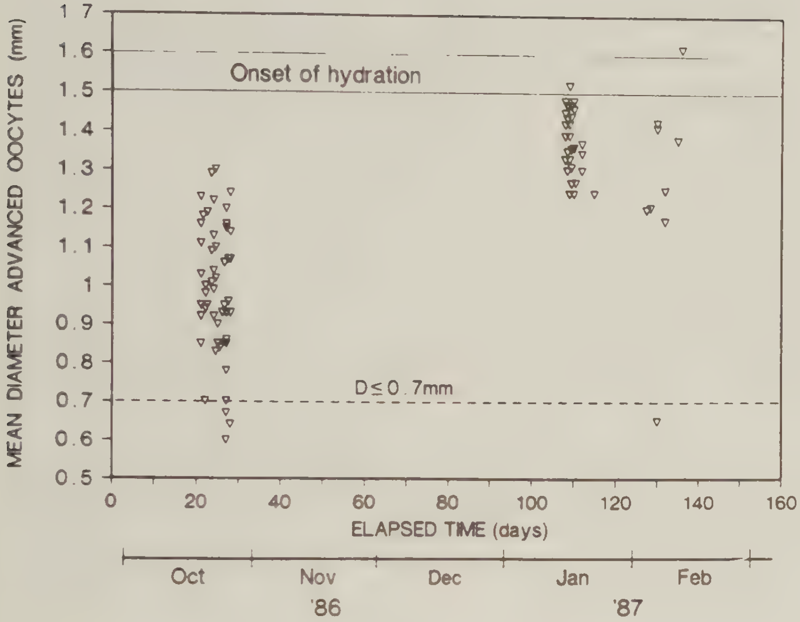


Figure 7. Mean diameter (D) of advanced oocytes in sablefish ovaries as a function of elapsed time (T) in days from October 6, 1986, to February 13, 1987. *Shaded area* indicates oocyte diameters at which the onset of hydration occurs; total fecundity was not estimated for ovaries in which the mean diameter was ≤0.7 mm (*dashed line*).

standing stock during the spawning season. By the middle of January the mean diameter of the advanced oocytes was 1.34 mm, which is close to the diameter at which hydration begins (1.5–1.6 mm) (figure 7). Thus by January, little maturation would be required to hydrate and spawn most of the advanced oocytes remaining in the ovary.

We compared the mean oocyte density (mean count of advanced oocytes in two tissue samples) to one calculated from the mean diameter by regressing mean oocyte density on the computed density $(1/6\ \pi\ D^3)^{-1}$ for fish taken in October and in January–February. In both sampling periods the intercept was very small and did not differ from zero. Assuming a zero intercept, the slope (K) was 0.94 for October and 0.88 for January–February. We tested the equality of the slopes by analysis of covariance (Zar 1974), and the results indicated that the slopes were not statistically different (t = 0.253, DF = 65). We combined the data from the two cruises to obtain a common slope of 0.94 (figure 8). K was less than one because samples of ovarian tissue contain material other than advanced oocytes (tissue fragments, postovulatory follicles, immature oocytes, etc.).

That K was nearly the same for fish taken in January–February as for those taken in October indicates that the fraction by weight of materials other than advanced oocytes in the tissue samples remained constant over the season, even though many of the females taken in January–February had spawned some of their oocytes. This indicates that postovulatory follicles are resorbed relatively rapidly after each spawning, and no major proliferation of vitellogenic oocytes had occurred. The relationship between observed oocyte density and the one computed from oocyte diameter was more variable for fish taken in January–February than in October: r^2 = 0.55 for January–February and 0.91 for October. Ovaries containing postovulatory follicles were substantially below the 0.94 line (figure 8, insert), indicating that the higher variability in January–February was probably caused by the occurrence of ovaries in which postovulatory follicles had not been resorbed.

The mean diameter of the advanced stock of oocytes was inversely correlated with total fecundity. A stepwise multiple regression of total fecundity (F_T, all data, October–February) on female weight (W), oocyte diameter (D), and elapsed time (T, during the spawning season) indicated that the diameter explained more of the variation in fecundity over the spawning season than did elapsed time (table 4). The final equation was

$$F_T = 351{,}992 + 71.4\ W - 263{,}462\ D,$$

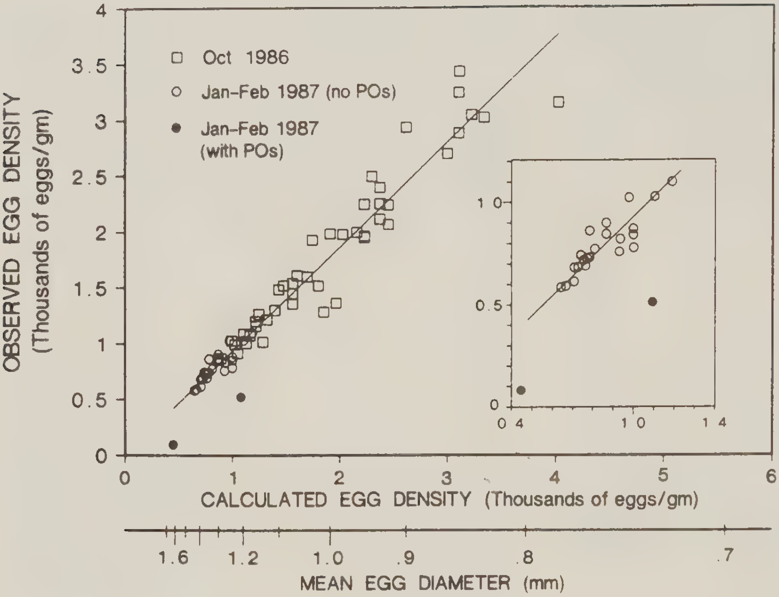


Figure 8. Relation between mean density of advanced oocytes in the ovary (Y axis) and density of oocytes calculated from the average diameter (X axis). The average diameter is calculated using the volume of a sphere and assuming oocyte specific gravity of 1.0:

$$C = K \frac{1}{\frac{1}{6} \pi D^3}$$

For October 1986 data (*squares*), $K = 0.91$; for February 1987 data (*open circles*), $K = 0.89$; and $K = 0.94$ for all data combined (*line*). Inset shows 1987 data in greater detail; *solid circles* represent ovaries with postovulatory follicles

where $R^2 = 0.61$ (T was deleted as a variable because its contribution to R^2 was negligible when diameter was included in the equation). Thus the mean diameter of the remaining advanced stock of oocytes appeared to be a better index of losses of oocytes due to spawning than was elapsed time. Diameter was also a significant variable in the fecundity equation when only the specimens taken in October were considered. The inclusion of diameter as a variable increased R^2 from 0.49 for female weight alone to 0.66, yielding the equation

$$F_T = 278{,}114 + 127\,W - 317{,}198\,D.$$

We assumed that the ovaries of females taken in October for fecundity estimation were in a prespawning state. That the mean diameter of the advanced oocytes was inversely correlated with fecundity may indicate that some losses due to spawning may have occurred in some of our October specimens.

DISCUSSION

Sablefish Reproduction

Unlike many pelagic fishes such as anchovy, sardine, tunas, and mackerels, the standing stock of advanced yolked oocytes in sablefish is equivalent to the total potential fecundity; in other words, fecundity is determinate. Five lines of evidence support this view. (1) In mature ovaries (mean diameter of advanced oocytes >0.7 mm) a hiatus exists between the advanced stock of mature oocytes and smaller immature oocytes (this hiatus is obvious in our figure 1, and Mason [1984] provides many more illustrations). (2) The standing stock of advanced oocytes declined over the spawning season. (3) The standing stock of advanced oocytes was lower in females having postovulatory follicles. (4) The mean diameter of the oocytes in the standing stock increased over the spawning season. (5) Our estimates of batch fecundity, total fecundity, and numbers of advanced yolked oocytes in hydrated ovaries were consistent with the assumption of determinate fecundity.

Two uncertainties exist. Our analysis does not rule out the possibility that more than one stock of advanced oocytes might be developed and spawned in succession during the year. The extent to which the potential total fecundity is realized is also uncertain. However, the low incidence of atretic oocytes in our specimens indicated that the realized and potential fecundity may have been similar in 1987.

The total potential fecundity of sablefish from central California was about twice that of fish from Canadian waters (Mason 1984; Mason et al. 1983),

TABLE 4

Summary of Stepwise Regression of Total Fecundity on Ovary-Free Female Weight (*W*), Mean Oocyte Diameter (*D*), and Elapsed Time (*T*) and Analysis of Variance Table for Second Step with Independent Variables *W* and *D*

Stepwise regression

Step	1	2	3
Constant	13785	351992	340087
W	84.2	71.4	70.7
t-ratio	6.76	7.18	6.90
D		−263462	−248948
t-ratio		−7.08	−4.10
T			−85
t-ratio			−0.30
S	85664	67260	67655
R^2	36.67	61.45	61.50

Analysis of variance

Source	DF	SS	MS	*F*	*P*
Regression	2	5.62×10^{11}	2.81×10^{11}	62.18	<0.0005
Error	78	3.53×10^{11}	4.52×10^{9}		
Total	80	9.15×10^{11}			

Source	DF	SEQ SS
W	1	3.36×10^{11}
D	1	2.27×10^{11}

but the length of females at maturity was about the same. This difference in fecundity could be due to differences between the regions. It is also possible that spawning may have been well underway when the Canadian fish were sampled, thus biasing Mason's estimates downward.

Sablefish from central California require about three spawnings to exhaust their standing stock of advanced oocytes; the last spawning batch is smaller than the first two. We are currently preparing a manuscript on reproduction of Dover sole (*Microstomus pacificus*), a species that lives and spawns in the same habitat as sablefish. The fecundity of Dover sole is determinate; relative to their weight, Dover sole have about the same fecundity as sablefish, but they spawn more frequently (9 or more times per year) and have a lower batch fecundity for their body weight. Thus spawning rate is an important life-history variable even in fishes with determinate fecundity.

Perhaps one of the more interesting unanswered questions concerning reproductive biology of sablefish is how a species that lives and spawns far below the penetration of significant sunlight is able to synchronize its spawning with season and possibly time of day. The reproductive energetics of such fishes as sablefish and Dover sole that live and reproduce in the cold and poorly oxygenated water of the oxygen minimum zone also seem of particular interest.

Fecundity Methodology in General

In this section we make a few comments on the analysis of fishes with determinate fecundity. The time of sampling is of key importance in estimating the total potential annual fecundity in sablefish, and probably in most fishes with determinate fecundity. Estimates will be biased if one samples either too early in the spawning season or too late. If one samples too early, the advanced stock may not have matured enough to be completely separate from the smaller immature oocytes, and consequently estimates may be imprecise or biased. We avoided this problem in sablefish by excluding ovaries in which the mean diameter of the advanced oocytes was 0.7 mm or less.

If one samples too late, spawning will have begun, the stock of advanced oocytes will have been reduced, and the total potential fecundity will be underestimated. In sablefish this bias could be large, since a single spawning batch may be a third or more of the standing stock. The possibility that such a bias may exist is usually not mentioned. Some authors may assume that in fishes with determinate fecundity all oocytes are spawned in one batch, or spawning is so frequent that capture of fishes with a partially expended stock of oocytes would be rare. This is not true for sablefish, because females with partially depleted stocks of oocytes were common during the spawning season. In fact, we do not know if our October estimate for sablefish was underestimated because of spawning. One female with hydrated oocytes was taken during the October cruise, indicating that spawning had begun by October. In addition, the inverse correlation of oocyte diameter and fecundity may indicate that some of the October females had spawned.

Accurate measurement of the diameter of advanced oocytes, counts of hydrated oocytes, and occurrence of postovulatory follicles were useful in validating and interpreting sablefish fecundity estimates. Using these measurements to estimate spawning rates for anchovy and other fishes with indeterminate spawning has become routine (Hunter et al. 1985), but their application to determinate spawners is new. Computation of the mean diameter of the oocytes constituting the advanced stock is usually not included in most fecundity studies. This procedure not only provided a quantitative method for selecting fish for fecundity estimates but was also useful in interpreting and validating our fecundity estimates. The mean diameter of the advanced oocytes increased during the spawning season, was inversely correlated with fecundity, and the reciprocal of the oocyte diameter was proportional to the density of oocytes in the ovary. These relationships helped substantiate the assumption of determinate fecundity. In addition, diameter measurement under certain circumstances may be a rapid method for estimating oocyte density and hence fecundity for determinate spawners.

The mean diameter of the advanced stock of oocytes is also the most accurate measure of ovarian maturity. Our histological analysis of sablefish ovaries indicated that hydration begins when the diameter of the yolked oocyte is 1.5–1.6 mm; investment of yolk ceases at this point, and the remaining increase in oocyte volume is due primarily to water uptake. Thus the ovary can be considered to have a full energy content when all advanced yolked oocytes have a diameter of about 1.5 mm and no oocytes have been spawned. This is a condition we rarely, if ever, encountered. Ovaries in which the mean diameter of the advanced oocytes was close to 1.5 mm were taken late in the season, and some batches may have been spawned. The advanced stock of oocytes in ovaries collected early in the season, when spawning was unlikely, had a smaller average diameter (about 1.0 mm). If one were to use the weight of such early ovaries (dia. = 1.0 mm) as a measure of reproductive effort, it would be necessary to about triple the ovary weight to account for future investment of yolk during the spawning season. Thus even in a determinate spawner such as sablefish, gonad weight is an inaccurate measure of reproductive effort unless values are adjusted for maturity (oocyte diameter) and spawning losses.

ACKNOWLEDGMENTS

We thank Tom Dark and Norman Parks (Northwest & Alaska Fishery Center) for providing sablefish specimens and permitting our use of unpublished data from their 1986 sablefish survey. We thank Sandra Owen (California Department of Fish and Game) and Eric Lynn (Southwest Fisheries Center) for collecting sablefish, and Mark Drawbridge and Wayne Kicklighter (Southwest Fisheries Center) for laboratory assistance.

LITERATURE CITED

Cailliet, G. M., E. K. Osada, and M. Moser. 1988. Ecological studies of sablefish in Monterey Bay. Calif. Fish Game 74(3):132–153.

Fujiwara S., and D. G. Hankin. 1988. Sex ratio, spawning period, and size and age at maturity of sablefish *Anoplopoma fimbria* off northern California. Nippon Suisan Gakkaisihi 54:1333–1338.

Hunter, J. R., and S. R. Goldberg 1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:641–652.

Hunter, J. R., and B. J. Macewicz. 1980. Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning for the northern anchovy, *Engraulis mordax*, during the 1979 spawning season. Calif. Coop. Oceanic Fish. Invest. Rep. 21:139–149.

———. 1985a. Measurement of spawning frequency in multiple spawning fishes. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, R. Lasker, ed. NOAA Tech. Rep. NMFS-36, pp. 79–94.

———. 1985b. Rates of atresia in the ovary of captive and wild northern anchovy, *Engraulis mordax*. Fish Bull., U.S. 83:119–136

Hunter, J. R., N. C. H. Lo, and R. J. H. Leong. 1985. Batch fecundity in multiple spawning fishes. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, R. Lasker, ed. NOAA Tech. Rep. NMFS-36, pp. 67–77.

Mason, J. C. 1984. On the fecundity of the sablefish (*Anoplopoma fimbria*) in Canadian waters. Can. Tech. Rep. Fish. Aquat. Sci. No. 1290, 17 pp.

Mason, J. C., R. J. Beamish, and G. A. McFarlane. 1983. Sexual maturity, fecundity, spawning, and early life history of sablefish (*Anoplopoma fimbria*) off the Pacific coast of Canada. Can. J. Fish. Aquat. Sci. 40:2126–2134

MBC Applied Environmental Sciences., 947 Newhall St., Costa Mesa, CA 92627. 1987. Ecology of important fisheries species offshore California. Outer Continental Shelf Study, Minerals Management Service, U.S. Dept. Interior, MMS 86-0093, 251 pp.

Norris, J. G., J. Rowley, and S. B. Matthews. 1987. Analysis of four factors affecting the sablefish soft fish problem. Univ. Wash., School of Fish., Fish Res. Inst., FRI-UW 8715, 32 pp.

Phillips, J. B., and S. Imamura. 1954. The sablefish fishery of California II. Catch analysis. Pac. Mar. Fish. Comm. Bull. 3:23–37.

Sullivan, K. M. 1982. The bioenergetics of the sablefish (*Anoplopoma fimbria*) occurring off southern California and energy allocation during low-frequency feeding in deep-living benthopelagic fishes. Ph.D. thesis, Univ. California, San Diego, 237 pp.

Wathne, F. 1977. Performance of trawls used in resource assessment. Mar. Fish. Rev. 39:16–23.

Zar, J. H. 1974. Biostatistical analysis. Englewood Cliffs, N. J.: Prentice-Hall, 620 pp.

8932

Marine Mining, Volume 8, pp. 303–315
Printed in the UK. All rights reserved

0149-0397/89 $3.00 + .00
Copyright © 1989 Taylor & Francis

Effects of Marine Mining Dredge Spoils on Eggs and Larvae of a Commercially Important Species of Fish, the Mahimahi (*Coryphaena hippurus*)

PAUL L. JOKIEL

National Marine Fisheries Service
Southwest Fisheries Center
Honolulu Laboratory
Honolulu, HI

Abstract *Eggs and early larval stages of the pelagic fish* Coryphaena hippurus *(commonly known as mahimahi) can survive prolonged exposure to concentrations of suspended sediment that greatly exceed levels caused by marine mining, coastal construction, and ocean disposal of dredge spoils. Sediments do not appear to present a direct threat to the early life stages of this economically important species at concentrations and exposure times that might result from typical ocean mining and ocean dumping operations. Results of this study support conclusions of previous investigations on effects of sediment on inshore and freshwater fishes. Lack of detrimental effects has also been reported in similar studies involving effects on phytoplankton, zooplankton, and adult pelagic fish. The results must be viewed with caution because these experiments did not evaluate the impact of sediments on complex ecological interactions, and did not evaluate the impact of possible toxicants that could be associated with some types of waste.*

Keywords Sediment, turbidity, fish larvae, fish eggs.

Introduction

Ocean mining, large-scale coastal construction projects, and ocean dumping can increase the suspended load of sediments over large areas of ocean. Organisms inhabiting estuaries, rivers, and bays have evolved in an environment that is often subjected to naturally occurring conditions of high turbidity. In contrast, organisms of the tropical pelagic realm live in water that is very low in suspended matter. Studies on the environmental impact of mining operations on phytoplankton, macrozooplankton, and adult fish have been conducted (Ozturgut et al. 1980; Chan and Anderson 1981; Hirota 1981; Lavelle and Ozturgut 1981; Lavelle et al. 1982; Matsumoto 1984). The impact of particulates on the survival and growth of pelagic fish larvae has not been addressed adequately, as emphasized by Hirota (1981) and Matsumoto (1984). A review of available information led Matsumoto (1984) to the following conclusion: "Most of the changes to the environment resulting from mining, such as increased suspended sediment particles, reduced illumination due to turbidity, mixing of cold bottom water with surface water, and changes in trace metals, salinity, and oxygen levels of the surface water, are not extensive enough to endanger tuna and billfish eggs and larvae."

Present address: University of Hawaii at Manoa, Hawaii Institute of Marine Biology, P.O. Box 1346, Kaneohe, HI 96744.

Direct experimentation involving the effect of sediments on eggs and larvae of pelagi species has not been conducted previously. The present study was designed to develo preliminary data in this area. Lack of such data is due to difficulties involved in th laboratory culture of pelagic fish. The species chosen for this study was the dolphin *Coryphaena hippurus*, known as the mahimahi in Hawaii. This is a commercially important species of food fish throughout its range.

Methods

Experiments were conducted at the Kewalo Research Facility of the Southwest Fisheries Center Honolulu Laboratory, where the mahimahi has been cultured through its life cycle.

Production of Eggs and Larvae Used in the Experiments

Adult mahimahi brood stock was maintained at the Kewalo Research Facility in large circular tanks of 7.2 m diameter and 1 m depth. The tanks were supplied with a continuous flow of aerated seawater providing a turnover time of <1 h. The fish were maintained at water temperatures of 23–25 °C and fed a diet of squid, fish, and vitamins. The brood stock typically spawned every other day.

Mahimahi eggs are spherical (1.5–1.7 mm diameter) and buoyant. They were normally collected within an hour of spawning with a fine-mesh dip net as they floated near the surface. Eggs were transferred into cylindrical laboratory aquaria of 150 L volume that contained mildly aerated filtered seawater. Under these conditions the eggs hatch within 50–60 h after spawning. Newly hatched mahimahi larvae measure approximately 4.5–5.5 mm standard length. Marine microalgae, cultures of *Tetraselmis* sp. and *Isochrysis* sp., were added to maintain water quality. At 25–26 °C the yolk is absorbed within 2 days of hatching, so the tank was inoculated at that time with planktonic rotifer, *Brachionus* sp., at a concentration of approximately 2 mL^{-1}. This concentration of food was maintained throughout the entire experiment.

Selection of Sediment Types and Sedimentation Levels to Be Tested

A marine mining operation (reviewed in Matsumoto 1984) typically has a discharge concentration on the order of 6 mg L^{-1} of suspended solids. Waste materials mix or sink rapidly in the water column, and are diluted within 15 min to a concentration of <1 mg L^{-1}. After 24 h the discharge plume dissipates to a concentration of <0.05 mg L^{-1}.

Typical ocean dumping operations of dredge spoils off Oahu caused a measurable increase in turbidity of the receiving waters for a relatively short period of 2–5 h (Environmental Protection Agency 1980), although a visually noticeable plume can sometimes persist for much longer (J. Naughton, personal communication). The highest concentration observed in the water immediately after dumping was 60 mg L^{-1} (Chave and Miller 1977). The suspended material in this case was rapidly dissipated to a concentration of 1 mg L^{-1} or less.

Suspended solid concentration in the surface waters immediately downstream of the Barbers Point channel dredging operation (February 1983 to October 1983) was approximately 20 mg L^{-1} or less (Harrison 1987). Again, this value rapidly diminished to levels of 1 mg L^{-1} or less as the plume dispersed offshore. The most turbid inshore waters found in Hawaii are in disturbed areas that have been previously dredged and filled (e.g., Honolulu Harbor, Oahu or Keehi Lagoon, Oahu). These worst-case situations typically have a maximum suspended solid load of approximately 6 mg L^{-1} (Chapman 1979), but these solids are quickly diluted to levels well below 1 mg L^{-1} as they are carried offshore by currents.

In sum, the highest concentration of suspended sediment resulting from ocean mining, ocean dumping, or coastal construction is between 5 and 50 mg L^{-1}, but these areas are highly localized. In general, larger areas of ocean are subjected to plumes with a suspended load of 1 mg L^{-1} or less of suspended solids. In those situations exposure times of larvae to concentrations of suspended solids of from 5 to 50 mg L^{-1} is probably less than 15 min, but prolonged (1–2 h) exposure to suspended solid levels of less than 1 mg L^{-1} could occur.

The initial tests described in this report were designed to exceed the anticipated typical environmental loading level of approximately 1 mg L^{-1} by several orders of magnitude. Six treatments were established with loading levels of 0, 500, 1000, 2000, 4000, and 8000 mg L^{-1}. These are the same concentrations used by Boehlert et al. (1983) and Boehlert and Morgan (1985) in studies of the effect of suspended solids on the eggs and larvae of the Pacific herring.

Incubation Chambers

One of the technical problems encountered in this study was the design of an apparatus that could keep the sediment suspended in the water while providing the low-turbulence conditions required for the maintenance of the larvae. An apparatus previously developed in a series of experiments on the effects of turbidity on feeding abilities of larvae of the Pacific herring (Boehlert and Morgan 1985) was employed in the initial tests. This apparatus consists of small (volume = 1 L) incubation chambers that are gently flushed with circulating seawater. The initial two experiments that evaluated effects of sediment on egg development on hatching were conducted in this apparatus. The chambers did not appear to influence egg development or hatching rate, but inflicted high mortality on the larvae of *C. hippurus*. Larger containers were developed for use in the larva tests. A series of four experiments was designed to compare 24-h larval mortality in the Boehlert and Morgan (1985) apparatus with mortality in large volume (30-L) chambers previously used at the Kewalo Research Facility to culture the mahimahi larvae. All *C. hippurus* larvae died within 24 h in the smaller chambers regardless of flow rate, level of turbulence, or age of larvae. Very low rates of mortality occurred in the 30-L control containers. Larvae of *C. hippurus* seem to be far more sensitive to mechanical damage than herring larvae. They were unable to withstand damage inflicted by bumping into the walls of small containers. Therefore, the larger containers were used in all tests involving larvae.

Sediment was suspended in the experimental system by placing an airstone in the vertex of the concave bottom. The containers used were 40 cm in diameter with vertical walls of 25 cm that sloped to a maximum depth of 30 cm in the center of the container. An air flow of 500 cm^3 min^{-1} created enough water motion to keep the clay and silt in suspension, while not damaging the larvae. Little or no sediment adhered to the steep container walls. The convection current induced by the airstone was sufficient to prevent settling of fine suspended material. Temperature was maintained at 26 ± 1 °C by holding the containers in a thermally regulated water bath. All experiments were conducted at the same level of controlled illumination (approximately 50 cm from fluorescent 40-W tubes). An artificial day-night cycle (13 h on and 11 h off) was maintained throughout the experiment.

Sediment Types

Several types of sediment were tested. Different materials that are representative of potential pollutants in the pelagic environment of the larval mahimahi were tested. These included sediments typical of the type produced by coastal construction, dredging for harbor construction and maintenance, ocean mining, and ocean dumping. Most of these materials are chemically inert minerals. Potential toxins and high organic biochemical oxygen demand could be a problem with certain sediments (i.e., as harbor dredge spoils). Grain-size distribution of all materials used in these experiments was determined with a Coulter counter using the method of Hirota (1981). Results of the sediment analysis are shown in Table 1. A description of these sediments follows.

Kaolin. This form of hydrated aluminum silicate is one of the primary end weathering products of volcanic rock and ferromagnesian minerals. A pure form of this silicate clay (Sigma Chemical Company K-73752) consisting of particles in the 0.1- to 4-μ size range was used in these experiments.

Bentonite (Montmorillonite). This aluminum-magnesium silicate clay is another of the primary weathering products of volcanic rock and ferromagnesian minerals. In the weathering series it is a precursor of kaolin. A pure form of this clay (Sigma Chemical Company B-3378) was used. This clay has a high swell-to-shrink ratio and is often used to seal water reservoirs against seepage.

Table 1
Results of Coulter Counter Analysis of Size Distribution for Material Used in These Experiments

Sediment size fraction (μm)	Sediment type[a]						
	R	P	M	K	C	D	B
1.30–1.59	0.2[b]	2.5	2.2	61.1	1.5	6.2	16.9
1.60–1.99	0.0	3.4	2.9	27.3	2.0	9.0	16.6
2.00–2.49	0.3	4.8	7.1	8.5	3.9	13.3	15.2
2.50–3.19	0.5	6.8	10.0	2.5	7.0	15.7	13.6
3.20–3.99	0.7	8.0	10.3	0.7	10.9	13.3	10.7
4.00–4.99	1.0	9.2	10.0	0.3	15.7	11.6	8.7
5.00–6.29	2.5	10.0	8.6	0.1	15.7	9.1	4.8
6.30–7.99	6.0	0.6	9.2	0.2	4.7	6.8	4.1
8.00–10.19	13.4	10.6	9.3	0.7	9.0	5.0	4.0
10.10–12.69	23.1	9.0	8.7	1.3	7.8	3.5	3.0
12.70–15.99	24.8	6.8	8.3	1.6	5.8	4.3	2.2
16.00–20.19	15.2	7.5	6.4	0.0	3.3	0.2	0.1
20.20–25.39	7.3	7.6	4.6	0.0	1.4	2.1	0.6
>25.4	5.1	3.1	2.8	0.0	1.3	0.0	0.1

[a] B = bentonite; C = calcareous ooze; D = dredgings from Barbers Point Deep Draft Harbor; K = kaolinite; M = manganese crust; P = dredgings from Pearl Harbor; R = red clay.

[b] Values in table are % of total sample within each size range.

Pelagic Carbonate Clay. Calcarious ooze dredged from near Gardiner Pinnacles was used in these experiments. It is typical of material that might be brought to the surface of the ocean during ocean mining operations at shallower depths.

Pelagic Red Clay. Red clay dredged from near Gardiner Pinnacles was used as a typical sediment from the deeper ocean that is commonly associated with manganese nodules.

Pulverized Manganese Crust. Samples of manganese crust taken from the exclusive economic zone in the northwestern Hawaiian Islands were pulverized into fine sediment with a mortar and pestle and passed through a 100-μm mesh sieve. The pulverized material represents one type of fine sediment that might result from an ocean mining operation.

Barbers Point (Oahu) Deep Draft Harbor Dredge Spoils. Mud was dredged from the bottom of the inner Barbers Point Deep Draft Harbor near the completion of dredging operations in July 1985. This harbor was dredged out of an emergent reef platform, and the dredge spoils consist almost entirely of carbonate materials. Organic matter was extremely low or absent in the spoils as indicated by lack of anoxia, even when the sediments were stored in a covered pail for many weeks. The material is a carbonate mud typical of that produced by dredging or erosion of coral reefs. The material was further fractionated by resuspension in water and the coarse fraction was allowed to settle within the fist 10 min. The water and suspended fine material was decanted into another container and allowed to fully settle.

Dredgings from Pearl Harbor, Oahu. Dredge spoils from harbors are commonly dumped at sea. Extensive sediment plumes result, with unknown consequences to the surrounding pelagic ecosystem (J. Naughton, personal communication). Material used in this study was dredged from the bottom of the main shipyard at Pearl Harbor, Oahu, Hawaii. This type of material differs from the others in that it has a higher organic content. Harbor dredgings often contain toxic substances as well, including heavy metals, hydrocarbons, and hydrogen sulfide.

Experimental Procedure

Drying can alter the chemical composition of sediments, so only moist samples of dredged materials and deep sea muds were used. The amount of moist sediment to be added to each treatment was calculated using measured wet to dry weight ratio for each sediment type. The proper amounts of moist sediment were preweighed and set aside. The sediments were reconstituted by mixing with seawater in a blender before being added to the experimental chambers.

Effects of Suspended Solids on Egg Survival, Development, and Hatching Rate

Experiment E-1 was designed to test the effect of sediment load on egg development. Sediment type was Barbers Point Deep Draft Harbor dredge tailings. The experiment was conducted in the chambers described by Boehlert and Morgan (1985) using four replicates each at six treatment levels (0, 500, 1000, 2000, 4000, and 8000 mg L^{-1}). Twenty fertile eggs (approximately 8 h postfertilization) were added to each of the 24 chambers. Duration of the experiment was 24 h, after which time the eggs were examined with a microscope for mortality or retarded development.

Experiment E-2 was run in the same manner as experiment E-1, except that fine kaolin was used as suspended solid, because the carbonate dredge tailings used in experiment E-1 did not produce egg mortality even at the extremely heavy loading of 8000 mg L^{-1}. Fine kaolin is very "sticky" and can adhere to surfaces.

Experiment E-3 was a continuation of experiment E-2, but the exposure time was extended from the original 24 h to a full 4 d of exposure to allow enough time for all eggs to hatch. We lengthened exposure time because no egg mortality occurred at 24 h, even at the highest concentration of 8000 mg L^{-1} of kaolin.

Effects of Suspended Solids on Larvae Mortality and Feeding

This series of experiments was designed to identify the most sensitive larval stage and also to identify possible differences in the impact of different types of sediment. All of the experiments on larvae were conducted in the same manner as described above using the larger containers of 30 L volume. The experimental aquaria were filled with 28 L of filtered seawater and allowed to equilibrate in the constant temperature water bath while being aerated at a rate of 500 cm^3 min^{-1}. Two liters of water were retained for later use in homogenizing sediment with a food blender and for rinsing the stock sediment from the blender into the experimental aquaria. Larval fish were gently added to each container since they are very easily damaged by handling. Mechanical damage was minimized by carefully scooping individual larvae from the rearing container into a bowl and gently placing them into the experimental chamber. For feeding larvae, the aquaria were stocked with rotifers at approximately 2 mL^{-1}. Sediment was then mixed into a slurry with a portion of the remaining liter of seawater in a commercial blender and slowly added to the experimental aquaria. The last portion of seawater was used to rinse the blender into the experimental aquarium.

The experiments differed from each other only in type of sediment, age of larvae, and exposure time. The differences between the various experiments are noted in Tables 3 and 4. Each experiment involved the use of six treatments run simultaneously. The series proceeded in a logical order, with each being based on results of the previous experiment. The experiments are extremely time-consuming, especially those involving larvae that were of feeding age. Also, the necessity of using very large containers to insure larval survival and limited space in the rearing laboratory precluded the use of multiple replicates. Therefore, it was necessary to run an experiment, review the results, and then plan the next experiment.

One important point must be emphasized. Long-term experience in the culturing of this fish species suggests that one can compare treatments only in a controlled experiment. All larvae must be taken from the same batch of eggs and all larvae used in an experiment must have been reared in the same container. Different batches of larvae can vary in sensitivity depending on many environmental, genetic, and nutritional factors that cannot be adequately predicted or controlled between batches. In work with such delicate fish larvae, mortality is often high within the control treatment. In general, the bioassay control should have less than 10% mortality (American Public Health Association 1985). The larvae must be transferred and counted, and some damage is inflicted, even with careful handling. Often there is a fairly high rate of mortality in newly hatched larvae, even without handling.

Results

General Observations

Egg Development, Mortality, and Hatching Rate. Nearly total egg survival was observed after 24 h in all treatments of experiment E-1 with no differences in rate of development, up to and including the highest sediment loading of 8000 mg L^{-1} (Table 2). The sediment used in the first experiment was carbonate material dredged from the Barbers Point Deep Draft Harbor on Oahu. In experiment E-2, eggs were examined periodically but did not show differences in development rate. In experiment E-3, egg hatch was nearly 100% in all treatments, as inferred by the empty egg cases with circular escape holes. A few eggs failed to hatch, but these were not restricted to any treatment and did not seem to be related to sediment loading level. This line of investigation was terminated because we observed little or no effect of sediment on development rate, egg mortality rate, and hatching rate even after 96 h of exposure to extremely high levels of suspended solids.

Larva Mortality Rate. Three facts are important in reviewing the results of the larval fish experiments presented in Tables 3 and 4. First, high mortality in control treatments was observed in some batches of larvae. Note results of experiments L-1, L-2, L-7, and L-8. Second, egg quality and the resultant larvae condition and survival may vary considerably among batches. We can legitimately compare results of treatments within an

Table 2

Summary of Egg Mortality and Hatching Data for Eggs of *Coryphaena hippurus*

Exp. No.	Stocking density (eggs L^{-1})	Sediment		Exposure time (h)	Egg mortality (%)	Normal egg development (%)
		Type[a]	mg L^{-1}			
E-1	1	D	0	24	0	100
			500	24	0	100
			1000	24	0	100
			2000	24	0	100
			4000	24	0	100
			8000	24	0	100
E-2a	20	K	0	24	0	100
			500	24	0	100
			1000	24	0	100
			2000	24	0	100
			4000	24	0	100
			8000	24	0	100
E-2b	20	K	0	96	5	100
			500	96	0	100
			1000	96	7	100
			2000	96	0	100
			4000	96	2	100
			8000	96	10	100

[a] D = dredgings from Barbers Point Deep Draft Harbor; K = kaolinite.

Table 3
Summary of Mortality Data for Larvae of *Coryphaena hippurus*

Exp. No.	Larva age (d)	Sediment		Time (h)	Larva mortality (%)
		Type[a]	mg L^{-1}		
L-1	0	K	0	2	14
			500	2	16
			1000	2	22
			2000	2	10
			4000	2	16
			8000	2	28
L-2	3	K	0	2	42
			500	2	—
			1000	2	20
			2000	2	12
			4000	2	30
			8000	2	50
L-3	0	B	0	2	0
			500	2	30
			1000	2	58
			2000	2	30
			4000	2	26
			8000	2	62
L-4	7	K	0	2	0
			500	2	4
			1000	2	4
			2000	2	0
			4000	2	12
			8000	2	12
L-5	3	B	0	2	0
			500	2	0
			1000	2	0
			2000	2	2
			4000	2	4
			8000	2	12
L-6	5	K	0	2	6
			500	2	30
			1000	2	26
			2000	2	26
			4000	2	52
			8000	2	100

Table 3 (*continued*)

Exp. No.	Larva age (d)	Sediment		Time (h)	Larva mortality (%)
		Type[a]	mg L^{-1}		
L-7	3	K	0	24	20
			500	24	17
			1000	24	6
			2000	24	17
			4000	24	14
			8000	24	17

[a] B = bentonite: K = kaolinite.

experiment, but not between experiments. Third, the sediment loading was set at levels that are orders of magnitude greater than actual field loading values. There is a very large margin for error when applying the resulting mortality data (i.e., no mortality observed at high levels of sediment loading) to the real-world situation. In addition, the experimental fish larvae were stressed somewhat by handling and presumably were in poor condition compared to their wild counterparts. In this respect the data are conservative and can be

Table 4
Summary of Mortality Data for Larvae of *Coryphaena hippurus* for Various Sediment Types

Exp. No.	Larva age (d)	Sediment		Time (h)	Larva mortality (%)
		Type[a]	mg L^{-1}		
L-8	4	None	0	24	26
		K	1000	24	68
		C	1000	24	54
		R	1000	24	32
		B	1000	24	100
		M	1000	24	46
L-9	7	None	0	2	0
		R	500	2	0
		R	1000	2	4
		M	500	2	0
		M	1000	2	4
		K	500	2	0
L-10	7	None	0	2	8
		P	500	2	8
		P	1000	2	6
		P	2000	2	0
		P	4000	2	3
		P	8000	2	11

[a] B = bentonite: C = calcareous ooze: K = kaolinite: M = manganese crust: P = dredgings from Pearl Harbor: R = red clay.

applied to field situations where the larvae are probably more capable of withstanding sediment stress.

In many of the experimental runs (experiments L-4, L-5, L-9, L-10), we observed little or no mortality at extremely heavy loading (1000 mg L^{-1} or more) of red clay, manganese crust, dredged material from the Pearl Harbor Shipyard area, kaolin, and bentonite. In other runs, we observed higher mortality that seemed to be related to the condition of the animals rather than the experimental treatments (experiments L-1, L-2, L-6, L-7, L-8). In either case the presence of extremely heavy loading of suspended solids had little apparent effect on the pattern of mortality.

An anomalous situation occurred in experimental treatments containing bentonite. This clay is atypical because it swells when wet and can form flocs when put into suspension. The flocs appeared to trap larvae and caused higher mortality (experiments L-3 and L-8). For reasons that we cannot explain, bentonite did not cause excessive mortality in experiment L-5. Perhaps the larvae were originally in better condition. In any event, this area needs more investigation. Any type of ocean mining or ocean dumping operation that precipitates flocs will be a cause of greater concern.

Larval Feeding Rate. Gut content analysis indicates that high concentrations of suspended solids severely impacted the ability of larvae to feed in the 2-h exposure (Table 5, experiment L-6) and the 24-h exposure (Table 5, experiment L-7). Even a 2-h reduction in feeding could be a serious problem for larvae in poor nutritional condition. Feeding inhibition appeared to be the cause of the 100% mortality in experiment L-6 after 2 h at the 8000-mg L^{-1} treatment level.

Larval Behavior in Relation to Sediment Plumes. During the course of the above experiments, it became apparent that the fish larvae were capable of rising above a turbidity plume. Larvae would rise to the surface as sediment slurry was slowly being added to the containers. Larvae caught by the plume quickly moved vertically into water above

Table 5

Feeding Activity (gut contents) at Various Sediment Concentrations for Larvae at Conclusion of Experiments L-6 and L-7

Exp. No.	Sediment concentration (mg L^{-1})	Gut contents: Rotifers	Cysts	Total items
L-6	0	16.3	3.1	19.4
	500	21.1	3.9	25.0
	1000	2.0	1.6	3.6
	2000	0.9	0.9	1.8
	4000	1.4	1.7	3.1
	8000	0	0	0
L-7	0	21.0	2.6	23.6
	500	9.1	1.4	10.5
	1000	3.2	1.6	4.8
	2000	0.8	0.4	1.2
	4000	2.6	2.2	4.8
	8000	0.6	1.0	1.6

the turbid layer. Aeration produced a gentle current in the containers that kept the larvae mixed throughout the water column. As soon as aeration was terminated, the sediments would begin to settle and the larvae would rapidly move into the clear water at the surface.

Discussion

Results of this investigation suggest that eggs and larvae of this fish are not extremely sensitive to the increased loading of sediment that might result from marine mining, ocean dumping, or coastal construction. As stated earlier, such activities might produce maximum loading levels of from 5 to 50 mg L^{-1} of suspended solids at the point of discharge, but sediment concentration decreases rapidly as the plume disperses. High concentrations are extremely localized (to within a few hundreds of meters from the discharge point) and do not persist very long (perhaps for 15 min) before mixing diminishes concentration to a few milligrams per liter. The increased density of water containing the solids leads to rapid sinking. Waves and currents rapidly disperse the remaining solids. A realistic loading level for a large plume is on the order of 1 mg L^{-1}. Eggs of *C. hippurus* were cultured at extremely high levels of suspended solids (up to 8000 mg L^{-1}) throughout the entire development time without any apparent increase in mortality or lowering of hatching success. Similar results on other species have been reported (Boehlert et al. 1983). Likewise, larvae were relatively insensitive to extremely heavy loading exceeding 500–1000 mg L^{-1} for a wide range of sediment types that most commonly impact the pelagic realm because of human activity. The results of these experiments with eggs and larvae of the mahimahi are consistent with results of a larger body of literature on effects of suspended solids on other pelagic biota. Failure to inflict mortality even at extremely high concentrations of sediment led to discontinuation of this experimental series.

Suspended solid concentration did not influence mortality in most situations, but did have a dramatic impact on feeding rate, as previously shown by Boehlert and Morgan (1985) for the Pacific herring. However, available field data suggest that real-world turbidity plumes will not be of sufficient density or persistence to severely impact larval feeding rate.

Larvae have a very limited swimming ability and would seem to be unable to avoid sediment plumes. We noted that although horizontal swimming speed is low in larval fishes, their vertical rate of movement (sinking or rising) can allow them to easily escape plumes in stratified water masses. The vertical movement required to escape a surface plume is only a matter of a few meters, whereas horizontal movement needed to escape the spreading of a plume might be on the order of hundreds of meters.

In conclusion, heavy loading of various types of sediments did not appear to inflict mortality on eggs or larvae of mahimahi. This general observation is in agreement with the conclusions of other workers such as Hirota (1981), who conducted experiments with zooplankton, and Matsumoto (1984), who summarized existing data on fishes and fish larvae. As stated by Scarratt (1987), "Virtually no evidence exists of adverse impacts from ocean mining on Canadian fisheries, but projections from other marine activities such as fishing itself, dredging, and other marine discharges give reason for caution." Effects of human activity on modification of these parameters might have a far greater impact on fish stocks than the direct effect of high levels of sediments. Data produced in the present study, however, must be viewed with some caution. Ellis (1987) discusses the four major impacts of turbidity, seabed smothering, contamination, and toxicity caused by marine mining. Further, he points out that we must evaluate the derived impacts of reduced biological production, biomagnification, and food pathology as well as stock mortalities. Further studies in many of these areas will be required.

Acknowledgments

Samples of pelagic red clay, carbonate ooze, and manganese crust were provided by E. DeCarlo. Dredgings from Pearl Harbor, Oahu, were provided by D. Somerton. Size grain analysis of suspended material used in the experiments was done by J. Finn. R. Y. Ito and T. K. Kazama provided support throughout the investigation in rearing the larvae and their food. G. Boehlert provided valuable guidance in the design of the experiments and offered many constructive observations on the original manuscript.

References

American Public Health Association. 1985. *Standard methods for the examination of water and wastewater*, 16th ed. Washington, DC: American Public Health Association. 1268 pp.

Barry, M. 1978. Behavioral response of the yellowfin tuna, *Thunnus albacares*, and kawakawa, *Euthynnus affinis*, to turbidity. Springfield, VA: U.S. Department of Commerce. National, Technical Service, NTIS Rep. No. PB/297106/AS.

Boehlert, G. W., and J. B. Morgan. 1985. Turbidity enhances feeding abilities of larval Pacific herring, *Clupea harengus pallasi*. *Hydrobiologia* 123:161–170.

Boehlert, G. W., J. B. Morgan, and M. M. Yoklavich. 1983. Effects of volcanic ash and estuarine sediment on the early life history stages of the Pacific herring, *Clupea harengus pallasi*. Water Resources Institute Technical Report WRRI-87, Oregon State University, Corvalis. 72 pp.

Chan, A. T., and G. C. Anderson. 1981. Environmental investigation of the effects of deep-sea mining on marine phytoplankton and primary productivity in the tropical eastern North Pacific Ocean. *Marine Mining* 3:121–149.

Chapman, G. A. 1979. Honolulu International Airport reef runway post-construction environmental impact report. Vol. 2. Technical report to the Department of Transportation, Air Transportation Facilities Division, Hawaii. 137 pp. Prepared for State of Hawaii by Parsons.

Chave, K. E., and J. N. Miller. 1977. Baseline studies and evaluation of the physical, chemical, and biological characteristics of nearshore dredge spoil disposal, Pearl Harbor, Hawaii. Final report. Prepared for Pacific Division Naval Facilities Engineering Command, Honolulu, Hawaii. Environmental Center, University of Hawaii. 184 pp.

Ellis, D. V. 1987. A decade of environmental impact assessment at marine and coastal mines. *Marine Mining* 6:385–417.

Environmental Protection Agency. 1980. Environmental Impact Statement (EIS) for Hawaii dredged material disposal sites designation. Prepared by the U.S. Environmental Protection Agency, Oil and Special Materials Control Division, Marine Protection Branch, Washington, DC 20460. 276 pp.

Harrison, J. T. 1987. The 40 MWe OTEC plant at Kahe Point, Oahu, Hawaii: A case study of potential biological impacts. National Oceanic and Atmospheric Agency, Technical Memorandum 68, National Marine Fisheries Service, Southwest Fisheries Center. NOAA-TM-NMFS-SWFC-68. 105 pp.

Hirota, J. 1981. Potential effects of deep-sea minerals mining on macrozooplankton in the North Equatorial Pacific. *Marine Mining* 3:19–57.

Lavelle, J. W., and E. Ozturgut. 1981. Dispersion of deep-sea mining particulates and their effect on light in ocean surface layers. *Marine Mining* 3:185–212.

Lavelle, J. W., E. Ozturgut, E. T. Baker, and S. A. Swift. 1982. Discharge and surface plume measurements during manganese module mining tests in the North Equatorial Pacific. *Marine Environmental Research* 7:51–70.

Matsumoto, W. M. 1984. Potential impact of deep seabed mining on the larvae of tunas and billfishes. U.S. Department of Commerce, National Oceanic and Atmospheric Agency Technical Memorandum. NMFS. NOAA-TM-NMFS-SWFC-44, 53 pp.

National Oceanic and Atmospheric Administration. 1981. Deep seabed mining. Final Programmatic Environmental Impact Statement. U.S. Department of Commerce, National Oceanic and Atmospheric Agency, Office Ocean Minerals and Energy, Washington DC, Vol. 1, 295 pp.

Ozturgut, E., J. W. Lavelle, O. Steffin, and S. A. Swift. 1980. Environmental investigation during manganese nodule mining tests in the North Pacific in November 1978. U.S. Department of Commerce, National Oceanic and Atmospheric Agency. Technical Memorandum, ERL MESA-48, 50 pp.

Scarratt, D. J. 1987. Fisheries interests and ocean mining. *Marine Mining* 6:141–147.

8933

Trends in Fishing Mortality Rate along with Errors in Natural Mortality Rate can cause Spurious Time Trends in Fish Stock Abundances Estimated by Virtual Population Analysis (VPA)

Michael F. Lapointe and Randall M. Peterman[1]

Natural Resource Management Program, Simon Fraser University, Burnaby, B.C. V5A 1S6 Canada

and Alec D. MacCall

Southwest Fisheries Center, National Marine Fisheries Service, 3150 Paradise Drive, Tilburon, CA 94920 USA

Lapointe, M. F., R. M. Peterman, and A. D. MacCall. 1989. Trends in fishing mortality rate along with errors in natural mortality rate can cause spurious time trends in fish stock abundances estimated by virtual population analysis (VPA). Can. J. Fish. Aquat. Sci. 46: 2129–2139.

Many researchers have reported biases in estimates of fish abundance reconstructed by virtual population analysis (VPA). We document that VPA can produce changing levels of bias through time, thereby creating spurious time trends in recruitment and stock biomass estimates. We generated catch data from empirically based simulations of nine fish populations, estimated abundances using VPA with a deliberately mis-specified natural mortality rate, *M*, and compared the estimates to the models' "true" abundances. A period of increasing fishing mortality rate, *F*, combined with an overestimate of *M*, produced spurious decreasing time trends in estimated abundance and recruitment, even when the true time series of *F* was known. Analogously, an underestimate of *M* led to a spurious increasing time trend. Bias was increased by a higher true *M*, and (for a given total change in *F*) by a slower increase in *F*. Because field estimates of *M* are uncertain and trends in *F* are common, some apparent trends (or lack of them) in abundances reconstructed by VPA may be artifacts. Therefore, inferences about the results of past management actions and about physical or biological effects on variability in recruitment must be made cautiously when VPA estimates are used.

De nombreux chercheurs ont signalé l'existence de biais dans les estimations des effectifs de poissons réalisées par l'analyse des populations virtuelles (VPA). Nous soutenons que les biais inhérents à l'exécution de la VPA peuvent varier dans le temps, introduisant ainsi de fausses tendances temporelles dans les estimations du recrutement et de la biomasse des stocks. Nous avons produit des données sur les captures à partir de simulations empiriques de neuf populations de poissons, estimé les effectifs au moyen de la VPA fondée sur un taux de mortalité naturelle délibérément faussé (*M*) et comparé les estimations aux effectifs « véritables » calculés par les modèles. Une période d'accroissement du taux de mortalité due à la pêche (*F*), alliée à une surestimation de *M*, a engendré des tendances temporelles anormalement décroissantes dans les estimations des effectifs et du recrutement, même quand la véritable série chronologique de *F* était connue. En corollaire, la sous-estimation de *M* a produit une fausse tendance temporelle croissante. Le biais augmentait quand le véritable taux de mortalité naturelle augmentait et quand la valeur de *F* croissait plus lentement (pour un changement total donné de cette valeur). Puisque les estimations de M sur le terrain sont peu sûres et que les tendances de la valeur de *F* sont courantes, la présence — ou l'absence — de tendances apparentes dans les effectifs établis par la VPA pourrait bien être artificielle. En conséquence, quand on utilise les estimations produites par la VPA, il importe d'user de prudence pour faire des inférences relatives aux résultats d'activités de gestion passées et aux effets des conditions physiques ou biologiques sur la variabilité des taux de recrutement.

Received November 17, 1988
Accepted August 1, 1989
(J9943)

Reçu le 17 novembre 1988
Accepté le 1 août 1989

Virtual population analysis (VPA) and related sequential population estimation techniques (Gulland 1983; Murphy 1965; Pope 1972; Rivard 1983; MacCall 1986) are widely used to reconstruct abundances of fish stocks. This reconstruction is an important component of standard procedures of many fisheries management agencies for estimating stock sizes, forecasting catches, and evaluating the success of past management schemes (Pope and Shepherd 1985; Rivard and Foy 1987).

The effects of using incorrect parameter values in VPA have been studied extensively (e.g. Pope 1972; Agger et al. 1973; Ulltang 1977; Sims 1984; Hilden 1988). It is well known from these and other papers that errors in the instantaneous natural mortality rate, M, and the instantaneous terminal fishing mortality rate, F_L, can create erroneous abundance estimates of both recruits and stock biomass, and that the effect of errors in F_L is reduced by large cumulative fishing mortality. In addition, errors in reported catches or in estimated weights and ages of fish can also lead to incorrect abundances (Pope and Gray 1983; Rivard 1983; Rivard and Foy 1987). Because of these sources of error, several authors have derived confidence intervals for abundances estimated by VPA under various types of uncertainty in inputs to VPA (e.g. Pope 1972; Prager and MacCall 1988; Sampson 1987, 1988; Kimura 1989). Under certain conditions, errors in M, F_L or both can also create spurious time trends in abundance (Rivard 1983; Hilden 1988; Sampson 1988; Bradford and Peterman 1989); i.e. even if true recruits and stock biomass were constant, such errors in the parameters of VPA would lead to a time trend in abundance estimates. Time trends in estimated abundance are especially relevant for, (1) evaluations of past management regulations based on the estimated response of the population, and (2) research on mechanisms causing temporal variation in recruitment.

---

[1] Author to whom correspondence should be addressed

The purpose of this paper is to document a much wider range of situations than previously reported in which spurious time trends in estimated abundances can occur. Specifically, if there are increasing trends in F in any part of the time series of catch data, and if an error exists in the M used in VPA, abundances reconstructed by VPA will have a spurious time trend.

Increasing time trends in F are common in many commercial fisheries (e.g. Hoag and McNaughton 1978; Anderson and Paciorkowski 1980; Winters et al. 1985; Espino and Wosnitza-Mendo 1986; Ahrenholz et al. 1987). These trends may result from a variety of mechanisms including increases in fleet size, "fishing-up" (the removal of accumulated stock, particularly old age classes) early in the development of a fishery (e.g. Ricker 1973; Francis 1986), use of nominal or incompletely standardized effort data which contain trends in fishing power, depensatory catchability coupled with decreases in stock size (e.g. clupeoids; MacCall 1976; Ulltang 1976), and others. Results from VPA often show increasing time trends in fishing mortality rates. However, as we document below, VPA will not correctly identify or account for such trends if there is an error in one or more of the parameters input to VPA, because trends in F exaggerate the effect of those errors in a different way than documented previously. Hilden (1988) showed that increasing trends in F biased recruitment estimates obtained from VPA, but he did not quantify their effect on time trends in recruitment or total stock biomass estimates. Analysts can, in theory, delete data covering years of increasing F from a catch data set before running VPA, but in practice there may be too few years of data left after deletion to be useful.

Methods

In nature, the true abundance of a fish stock will always be uncertain. Therefore, to investigate the impact of increasing trends in F on VPA, we used a simulation model to generate synthetic (i.e. "true") abundances that were known exactly. We focused our analyses on trends of increasing F with time, because they are the most common.

Historical F trends have differed among stocks, varying from small to large ranges in absolute F and short to long periods over which F changes occurred. Therefore, to generalize our findings, we based our analysis on nine different stocks.

The general procedure was:

1. Generate a time series of simulated "true" abundance and catch data from a population model, using known parameters and a time series of increasing fishing mortality rates to simulate the trends in F (called an "F scenario").
2. Estimate annual abundances using iterative VPA (Rivard 1983) given: (a) the catches generated by the simulation of the population model, (b) the true time series of fishing mortality rates, and (c) an incorrect M^{VPA} (henceforth, parameters with a VPA superscript will refer to the parameter values input to VPA, and those without superscripts will be the true values used in the simulation to generate the catch data).
3. Compare time trends of estimated and true abundances (recruits and biomasses).

The specifics of this procedure are as follows.

Simulated Populations and F Scenarios

Simulated populations were generated using parameters (fishing and natural mortality rates, age-specific selectivities, and weights-at-age) from nine stocks (Table 1). We chose these stocks as examples of fishes with different life histories, age-specific selection coefficients, and F trends. We used the parameter values in Tables 2 and 3 as well as others drawn from the references in Table 1. Populations were simulated using the following approach.

Recruitment (number of fish in the youngest fished age) was assumed constant at 1×10^6 fish (we relax this assumption later in the Sensitivity Analysis section), and numbers of fish in older ages were calculated using

$$(1) \quad N_{i+1} = N_i \, e^{-Z_i},$$

where N is the initial number of fish of age i and $Z_i = M + F_i$. M and F_i are the instantaneous annual natural mortality rate and age-specific fishing mortality rate, respectively. We assumed that the population had been fished at the minimum F prior to the start of each F scenario (see below).

Age-specific fishing mortality rates were calculated as

$$(2) \quad F_i = s_i \, F_L,$$

where the s_i's are the age-specific selection coefficients and F_L is the fishing mortality rate for the oldest age in a given year. F_L's for each year were determined from scenarios used to simulate periods of increasing F (see below). By assuming that the time series of F_L was known exactly for VPA, we were able to document the minimum qualitative effects of errors in M^{VPA}. We relax this assumption of known F_L later.

Stock biomass in each year was calculated as

$$(3) \quad B_t = \sum_i N_i w_i,$$

where w_i are the weights at each age in kilograms.

Simulated catches were generated using the Baranov catch equation (Ricker 1975).

$$(4) \quad C_i = \frac{N_i \, F_i \, (1 - e^{-Z_i})}{Z_i},$$

where C_i is the number of fish caught at age i.

We used two different F scenarios. In the first scenario, we used increasing F trends estimated from the historical data for each stock, to explore the relative magnitude of potential bias in abundance estimates for historical situations. Each historical F pattern was approximated with a linear trend using the observed maximum and minimum F values ($F_{\max}$ and $F_{\min}$) and the actual number of years of increasing F observed for each stock (Table 3). In the second scenario, we applied a common F trend to all stocks to generalize our results by exploring how the bias in estimated abundances was affected by different life history characteristics. In both F scenarios, F_L for each year was calculated using

TABLE 1. Sources of data used to generalize effects of input errors to VPA across stocks.

Common name	Location	Species	Abbreviation	Source
Atlantic mackerel	ICNAF areas 3–6	*Scomber scombrus*	Mac	Anderson and Paciorkowski (1980)
Atlantic menhaden	East coast, US.	*Brevoortia tyrannus*	Men	Hightower and Grossman (1985) Arenholz et al. (1987)
Dover sole	Oregon	*Microstomus pacificus*	Dov	Hayman et al. (1980)
Fortune Bay herring	Fortune Bay, Nfld.	*Clupea harengus*	FBH	Winters et al. (1985)
Pacific cod	Hecate Strait, B.C.	*Gadus macrocephalus*	Cod	Fournier (1983)
Pacific halibut	Area 3	*Hippoglossus stenolepis*	Hal	Hoag and McNaughton (1978)
Pacific ocean perch	Queen Charlotte Sound, B.C.	*Sebastes alutus*	POP	Hightower and Grossman (1985) Archibald et al. (1983)
West Scotland herring	ICES area VIa	*Clupea harengus*	WSH	Saville and Bailey (1980)
Yellowfin sole	Eastern Bering Sea	*Limanda aspera*	Yel	Wakabayashi (1984)

TABLE 2. Parameter values for nine different marine fish stocks used in the analysis. Abbreviations of stock names in the top row are defined in Table 1, where literature sources are also given. M is the instantaneous annual natural mortality rate. Selection coefficients (i.e. s_i) of partial recruitment to the fishery are given for each fished age, scaled so that the coefficient for the last fished age class is 1.0 in all cases. Unfished ages are shown by a hyphen.

	Stock								
	Mac	Men	Dov	FBH	Cod	Hal	POP	WSH	Yel
M	0.3	0.45	0.2	0.2	0.65	0.2	0.05	0.1	0.25
Age	Selection coefficients								
0	—	0.34	—	—	—	—	—	0.22	—
1	0.12	1.06	—	—	—	—	—	0.33	—
2	0.37	0.93	—	0.14	0.14	—	—	0.60	—
3	0.63	0.91	—	0.52	0.48	—	—	0.82	—
4	0.78	0.84	—	0.86	0.76	—	—	0.81	—
5	0.80	1.07	—	1.09	0.92	—	—	0.81	0.04
6	0.77	1.00	0.48	1.08	1.00	—	0.05	0.85	0.17
7	0.92	1.00	0.61	1.07	1.00	—	0.11	0.95	0.33
8	0.97	—	0.67	1.05	1.00	0.14	0.21	0.98	0.56
9	1.00	—	0.80	1.03	1.00	0.29	0.36	1.00	0.73
10	—	—	0.89	1.02	—	0.41	0.58	—	0.88
11	—	—	0.95	1.00	—	0.55	0.85	—	0.97
12	—	—	1.08	—	—	0.68	1.14	—	1.00
13	—	—	1.00	—	—	0.90	1.40	—	1.00
14	—	—	—	—	—	0.92	1.56	—	1.00
15	—	—	—	—	—	1.00	1.60	—	1.00
16	—	—	—	—	—	1.00	1.50	—	1.00
17	—	—	—	—	—	1.00	1.28	—	1.00
18	—	—	—	—	—	1.00	1.00	—	—
19	—	—	—	—	—	1.00	1.00	—	—
20	—	—	—	—	—	1.00	1.00	—	—
21	—	—	—	—	—	—	1.00	—	—
22	—	—	—	—	—	—	1.00	—	—
23	—	—	—	—	—	—	1.00	—	—
24	—	—	—	—	—	—	1.00	—	—
25	—	—	—	—	—	—	1.00	—	—
26	—	—	—	—	—	—	1.00	—	—
27	—	—	—	—	—	—	1.00	—	—
28	—	—	—	—	—	—	1.00	—	—
29	—	—	—	—	—	—	1.00	—	—

$$(5)\quad F_{L,t} = F_{L,t-1} + \left(\frac{F_{max} - F_{min}}{T_f}\right) \text{ for } t<T_f,$$

where $F_{L,t}$ is the fishing mortality in year t for the oldest age, T_f is the duration (years) of increasing F for each scenario, and $F_{L,0} = F_{\min}$ for all scenarios. For the historical scenarios, $F_{\min}$, $F_{\max}$, and T_f were different for each stock (Table 3). For the common F scenarios, all stocks had $F_{\min} = 0.1$, $F_{\max} = 1.0$, and T_f = one of the values between 5 and 30 yr, in 5-yr intervals. The purpose of varying T_f in different model runs of the common F scenarios was to explore the effects of a wide range of rates of change in fishing intensities (rapid to slow increases in F). For each T_f, we calculated the rate of change in F per year (i.e. $\Delta F{\cdot}\text{yr}^{-1} = [(F_{\max} - F_{\min})/T_f]$). In both the common and historical scenarios, we set $F_L = F_{\max}$ after the period of increasing F and for the remainder of the simulation (i.e. for all $t \geq T_f$).

Estimated Populations

Populations were estimated using VPA in the standard formulation shown below (Gulland 1983, p. 105). First, the number of fish in the oldest (L) age class in each year was estimated from

$$(6)\quad N_i = \frac{C_i\, Z_L^{\text{VPA}}}{F_L\,(1 - e^{-Z_L^{\text{VPA}}})},$$

where $Z_L^{\text{VPA}} = F_L + M^{\text{VPA}}$, and F_L for each year was determined from equation (5) above. Thus, we assumed that the true time series of F_L values was known. F_i values for each of the younger ages in each cohort were calculated by finding the solution to

$$(7)\quad \frac{N_{i+1}}{C_i} = \frac{Z_i^{\text{VPA}}\, e^{-Z_i^{\text{VPA}}}}{F_i\,(1 - e^{-Z_i^{\text{VPA}}})},$$

which comes from solving equation (1) for N_i, and substituting the result for the left hand side of equation (6). Equation (7) was solved for F_i using Muller's (1956) method available in the IMSL subroutine ZREAL1 (IMSL 1982). Starting values for the subroutine were estimated from

$$(8)\quad F_i = \log_e(N_i/N_{i+1}) - M^{\text{VPA}},$$

where the N_i was calculated using Pope's (1972) cohort analysis approximation,

$$(9)\quad N_i = N_{i+1}e^{M^{\text{VPA}}} + C_i e^{(M^{\text{VPA}}/2)}.$$

F_i values from solving equation (7) were then used in equation (10) along with M^{VPA} to solve for N_i

$$(10)\quad N_i = N_{i+1}/e^{-Z_i^{\text{VPA}}}.$$

This process was repeated for each cohort, working backwards in time in the usual fashion. We used the iterative method of Rivard (1983) in which new age-specific selection coefficients were calculated from the table of F_i estimates and the VPA was repeated until selection coefficients from successive iterations converged. The age-specific selection coefficients were used in

TABLE 3. For each of the nine stocks studied here, we show from left to right the assumed true instantaneous natural mortality rate, M, and six characteristics of the historical F scenarios: the observed minimum and maximum F (F_{min} and F_{max}), duration of the period of increasing F, range in cumulative F values between cohorts at the start and end of the period of increasing F, and the rate of change in F per year (unscaled and then scaled relative to M).

Stock	True M	F_{min}	F_{max}	Years of increasing F (T_f)	Range in cumulative F	$\Delta F \cdot yr^{-1}$	$\Delta F \cdot yr^{-1} \cdot M^{-1}$
Atlantic mackerel	0.30	0.05	0.85	10	2.074	0.08	0.27
Atlantic menhaden	0.45	0.70	3.00	6	4.359	0.38	0.85
Dover sole	0.20	0.12	0.25	9	0.371	0.01	0.07
Fortune Bay herring	0.20	0.02	1.00	6	1.408	0.16	0.82
Pacific cod	0.65	0.22	0.76	6	0.700	0.09	0.14
Pacific halibut	0.20	0.11	0.30	12	0.591	0.02	0.08
Pacific ocean perch	0.05	0.05	0.35	3	0.022	0.10	2.00
West Scotland herring	0.10	0.20	1.10	8	1.654	0.11	1.12
Yellowfin sole	0.25	0.08	0.29	4	0.040	0.05	0.21

equation (2) to calculate the terminal F values for incomplete cohorts (cohorts that had not yet reached the oldest fished age by the last, or most recent, year of the catch data). F_i values for younger ages of complete cohorts were obtained from equation (7) and remained unchanged after iterations. Thus, the iterative method we used only affected abundance estimates for the incomplete cohorts.

In each case, the time series of F_L's given to the VPA was identical to that used in the simulated population, and the catches were those generated by the simulation. The only error introduced into VPA was through the value of M^{VPA}; we used $M \pm 50\%$. We chose to solve the VPA equations exactly using the IMSL routine because with this range in errors, the incorrect M^{VPA} values for some stocks were outside of the range of acceptable values for either Pope's (1972) or MacCall's (1986) approximations.

Comparison of Estimated and True Abundances

We compared the true abundances with those estimated by VPA using the following index of percent spurious change, P_S,

$$(11) \quad P_S = P_E - P_T,$$

which was the difference between the percentage change in estimated abundances (P_E) over the course of the simulation and the percentage change in true abundances (P_T) over the same period. We used percent change as our index because it was a general measure of the bias that was also proportional to the absolute change per year in recruits or biomass. P_E and P_T were calculated as

$$(12) \quad P_E = \frac{NE_t - NE_1}{NE_1} \cdot 100$$

and

$$(13) \quad P_T = \frac{NT_t - NT_1}{NT_1} \cdot 100,$$

where NT_1 and NE_1 were the true and estimated initial abundances at time $t = 1$, respectively, and NT_t and NE_t were the stabilized abundances following the period of increasing F. The latter abundances occurred at time $t = T_f$ for recruitment, and $t = T_f + k - 1$ for biomass, where k is the number of ages fished for each stock. We generated catch data for $T_f + 2k - 2$ yr to ensure that stabilized abundances were estimated from cohorts that had reached the oldest fished age. Thus, we only used the abundance estimates obtained from "complete" cohorts in our calculations.

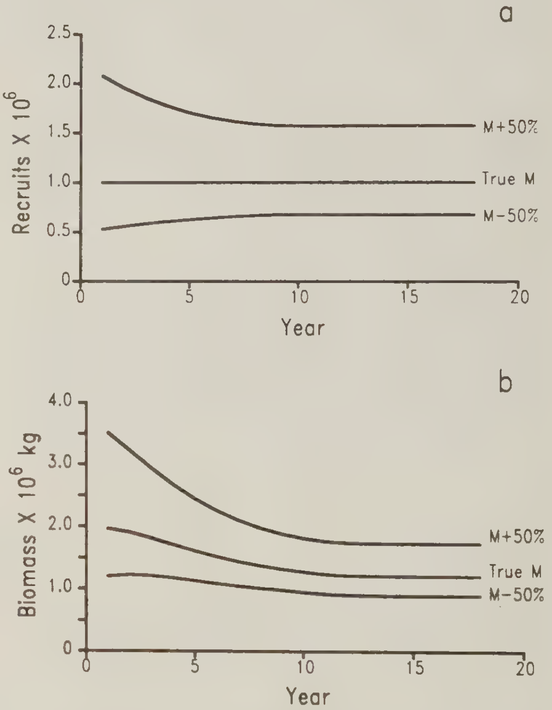


FIG. 1. Time series of Atlantic mackerel recruits and total stock biomass using the historical F trend for that stock. Part (a) shows true recruits (middle line) and recruits estimated by VPA when the natural mortality rate used in VPA (M^{VPA}) was 50% above the true value, M, (top line) or 50% below M (bottom line). Part (b) shows true stock biomass (middle line) and biomass estimated when M^{VPA} was 50% above M (top line) or 50% below M (bottom line). VPA estimation proceeded from the right side of the figure to the left.

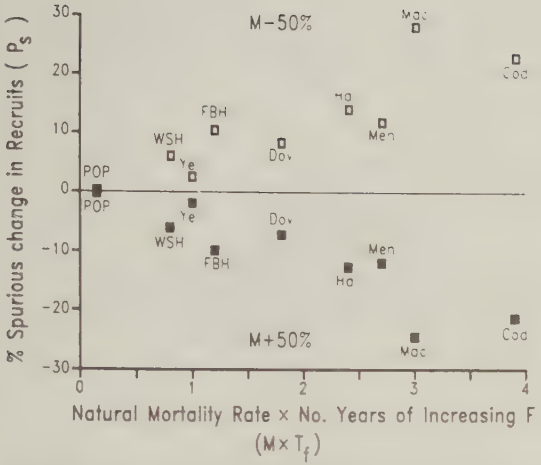


FIG. 2. Percent spurious change (increase or decrease) in abundance of recruits estimated by VPA when M^{VPA} was 50% below M (top half; $r^2=0.78$, $P<0.002$) or 50% above M (bottom half; $r^2=0.81$, $P<0.002$). Stock abbreviations are defined in Table 1. For each stock, the true M value, duration of the period increasing F (T_f), F_{min} and F_{max} are for the historical scenarios (Table 3).

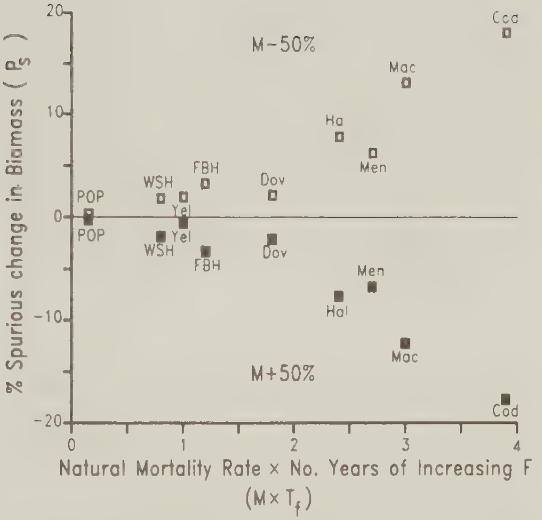


FIG. 3. Same as Fig. 2 except for stock biomass. For $M^{VPA}=M-50\%$, $r^2=0.86$, $P<0.001$ and for $M^{VPA}=M+50\%$, $r^2=0.88$, $P<0.001$.

We refer to P_T and P_E as the true and estimated change in abundance and P_S as the spurious change or spurious trend. We calculated each of these three quantities for both recruits and stock biomass. In the case of recruitment, $P_S=P_E$ because P_T, the true trend, was 0 (i.e. we assumed constant recruitment in our simulations). Thus, in our results below, $P_S>0$ for recruitment meant that VPA estimated a false increasing time trend in recruits, whereas $P_S<0$ would come from a spurious decreasing trend. However, for stock biomass, increases in F cause a decline in both the simulated (i.e. true) and estimated biomass as older age classes are depleted from the initial stock. Thus, $P_S>0$ for stock biomass meant that VPA underestimated the true percentage decline in biomass. For example, $P_E=-20\%$ for biomass and $P_T=-30\%$ gives $P_S=+10\%$ from equation (11). In contrast, $P_S<0$ indicated an overestimate of the decline in biomass.

Results

Historical *F* Scenarios

Figure 1 shows results for Atlantic mackerel (*Scomber scombrus*) at various M^{VPA} values when the historically observed F scenario was applied. When M^{VPA} equalled the true M, VPA correctly estimated the true recruitment and true stock biomass (middle lines in Figs. 1a and 1b). Therefore, trends in F do not cause VPA to estimate abundance incorrectly when M is known exactly and there are no other errors in VPA inputs. However, when M^{VPA} was incorrect, estimates of recruits and stock biomass diverged from the true values as VPA proceeded back in time through the cohorts (from right to left in Fig. 1). When M^{VPA} was less than M, recruitment and biomass were both underestimated, VPA generated a false increasing time trend in recruits, and underestimated the decreasing trend in biomass (Fig. 1). When M^{VPA} was greater than M, VPA generated spurious decreasing time trends in recruitment, overestimated the percent decline in biomass, and overestimated recruitment and stock biomass (Fig. 1). We found similar results for other stocks; for a given sign of error in M^{VPA}, the spurious change in recruits and biomass for the historical scenarios increased with the product of M and the number of years of increasing F, T_f (Figs. 2 and 3). When M^{VPA} was incorrect, the percent spurious change was greater for recruits than for total stock biomass for a given stock (Figs. 2 and 3).

Explanation of Historical *F* Scenarios

The underlying cause of the time-trend bias is a simple extension of the well-known effects of errors in VPA parameters (Pope 1972; Agger et al. 1973; Ulltang 1977; Sims 1984; Bradford and Peterman 1989; Sampson 1988; Hilden 1988). Pope (1972) showed that for a given M^{VPA}, errors in estimated abundance at a given age caused by an incorrect choice of $F_L{}^{VPA}$ decreased as the cumulative fishing mortality on the cohort increased. Pope's analysis was extended to include errors in M by Sims (1984), who gave an approximate formula that related the relative error in abundance estimates to the magnitude of error in M^{VPA} and cumulative fishing mortality (see Sims' equation 8). These results imply that identical successive annual cohorts that experience different cumulative fishing mortality rates will have different amounts of bias in recruitment estimates for each successive cohort when these estimates are derived from VPA with an incorrect $F_L{}^{VPA}$ or M^{VPA}.

Indeed, this is the underlying cause of the spurious time trends in abundance estimates shown in this paper; differences in cumulative fishing mortality rate exist among successive cohorts because of changes in F over time and these are coupled with an incorrect input parameter to VPA, M^{VPA}. This mechanism is detailed below.

A full explanation of the time-trend bias in Fig. 1 requires several steps. (1) For the case of $M^{VPA}=M+50\%$ in Fig. 1a, recruitment estimates in years 10 to 18 were constant but biased above true recruitment; this overestimate was due solely to the error in M^{VPA} because there was no change in F during this period. (2) However, the sequence of fishing mortality rates

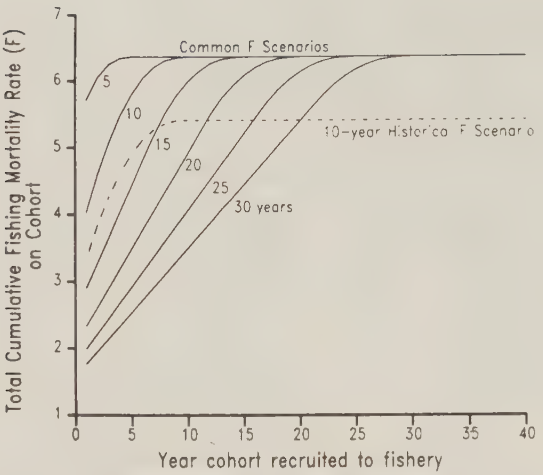


FIG. 4. Total fishing mortality rate (ΣF_t) experienced by each cohort of Atlantic mackerel in simulations using true M and F_L values. Lines are shown for each of the simulated common F scenarios (solid lines) ranging in duration from 5 to 30 yr, and for the 10-yr historical F scenario (dashed line). VPA estimation proceeded from the right side of the figure to the left.

during the period of increasing F caused cohorts that recruited to the fishery in years 1–9 to experience lower cumulative fishing mortality rates (ΣF_t for all fished ages) than cohorts that recruited later (dashed line in Fig. 4). As Sims (1984) noted, the amount of error in an abundance estimate resulting from an error in M^{VPA} is larger when the cumulative fishing mortality experienced by a cohort is small. Thus, the lower cumulative fishing mortality rates on cohorts that recruited in years 1–9 led to more biased abundance estimates in those years. (3) Finally, recruits from each successive cohort that recruited in years 1–9 were estimated with decreasing bias, because as F increased, cumulative fishing mortality rates on each successive cohort increased (Fig. 4 dashed line). In other words, the error in abundance estimates already present due to an incorrect M^{VPA} was exaggerated most in early years when cumulative F was low and least when cumulative F was high, at the end of the period of increasing F. Hence, the result was a time trend in estimated recruitment (Fig. 1a), despite a constant true recruitment and the use of the true time series of F_L by VPA. For brevity, we refer below to this mechanism that explains time trends as "differences in cumulative fishing mortality rate among successive cohorts." In the case of $M^{VPA} = M - 50\%$, the explanations are similar but errors appear as underestimates of true abundance rather than overestimates (bottom of Fig. 1a).

Time trends occur in stock biomass estimates (Fig. 1b) through the same mechanisms as in recruits. However, spurious time trends were generally greater for recruits than for stock biomass because estimates of abundance for younger ages will be more biased in percentage terms than estimates for older ages within the same cohort; as VPA works back through a cohort, these estimates of young ages result from more applications of the incorrect Z^{VPA} in equation (10). Total stock biomass estimates are less biased than recruits because biomasses are the weighted sum of abundances over ages, and the less biased estimates for older ages dilute the effect of the more biased abundance estimates of younger ages.

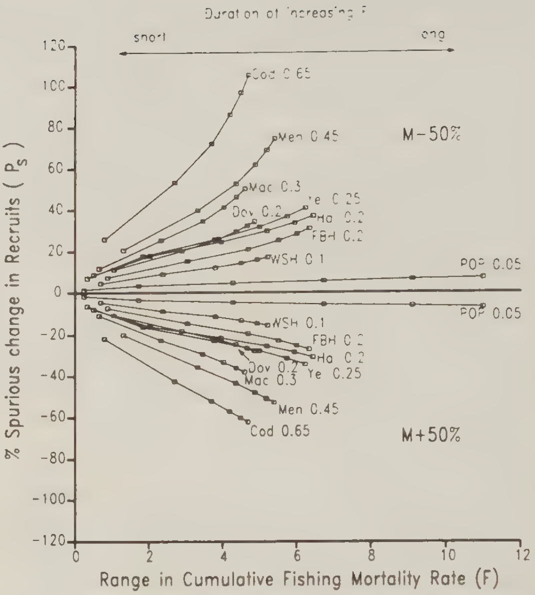


FIG. 5. Percent spurious change (increase or decrease) in abundance of recruits estimated by VPA when M^{VPA} was 50% below M (top half) or 50% above M (bottom half). Curves are for the stocks abbreviated on the right (defined in Table 1) and true M values are beside stock abbreviations. For each stock, the duration of the common F scenarios ranged from 5 yr (left point) to 30 yr (right point) in 5-yr intervals. "Range in cumulative fishing mortality rate" is the maximum cumulative F on cohorts minus the lowest cumulative F encountered in that F scenario (see text).

Spurious change in recruits and biomass increased with the product of M and T_f (Figs. 2 and 3) because for any given stock, longer periods of increasing F result in greater differences in cumulative fishing mortality among successive cohorts (Fig. 4), and because for any given cumulative F, larger M^{VPA} results in more bias (see section "Explanation of comparisons among stocks" below). Thus, $M \cdot T_f$ is an approximate index of the time-trend bias caused by an incorrect M^{VPA} for these historical situations. The index is not perfect because of differences in historical ranges in F and partial recruitment vectors among stocks (Tables 2 and 3).

Common F Scenarios

Comparisons among stocks

One purpose of the common F scenarios was to compare spurious time trends among stocks with different life history characteristics. This was not possible in the previous scenarios because of historical differences in F trends among stocks; in this section, we applied the same sequence of increasing F to all stocks. In these common F scenarios, F_{min} and F_{max} were the same for all durations of increasing F, ranging from 5 to 30 yr, as described above. Because time trends in abundance estimates caused by increasing trends in F in conjunction with an incorrect M^{VPA} result from differences in cumulative fishing mortality among successive cohorts, we calculated a single index of these differences, which was the cumulative fishing mortality rate on cohorts that recruited to the fishery in the year

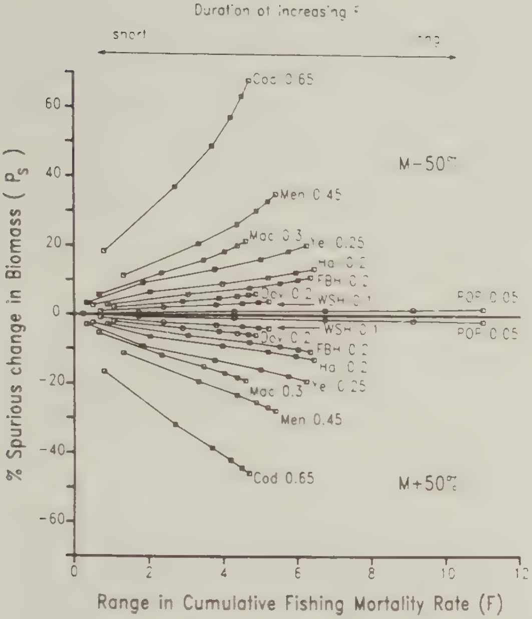


FIG. 6. Same as Fig. 5 except for stock biomass.

T_f (when $F_L=F_{\max}$) minus cumulative F on cohorts that recruited in year 1 (top minus bottom values on a given curve in Fig. 4). This index was specific to the stock and the number of years of increasing F because stocks had varying numbers of exploited age classes and different age-specific selection coefficients and because for any given stock the cumulative fishing mortality on cohorts varies with the numbers of years of increasing F (Fig. 4). We henceforth call this index "the range in cumulative F."

We used the range-in-cumulative-F index to compare the percent spurious change in recruits (Fig. 5) and stock biomass (Fig. 6) across stocks. For each stock, six square points are shown. Each point on a given curve is for a given duration of increasing F, ranging from 5 yr (left-most point on each curve) to 30 yr (right-most point). Long periods of increasing F resulted in the largest absolute values of percent spurious change in abundance estimates within a given stock. Stocks with larger M (e.g. Pacific cod (*Gadus macrocephalus*), menhaden (*Brevoortia tyrannus*)) had greater spurious trends for a given length of increasing-F period than stocks with low M. Trends for high M stocks were also more sensitive to changes in the length of the increasing-F period; high M stocks had a much larger increase in the absolute value of percent spurious change than low M stocks when the rate of change in F was varied from rapid (left ends of curves) to slow (right ends). Three stocks (i.e. Pacific halibut (*Hippoglossus stenolepis*), Dover sole (*Microstomus pacificus*) and yellowfin sole (*Limanda aspera*)) with similar M values had overlapping curves of percent spurious change in recruits. As found for the historical scenarios, recruits had larger absolute values of percent spurious change than biomass for a given situation.

Explanation of comparisons among stocks

First, within each stock, longer periods of increasing F caused larger absolute values of the percent spurious change in abundance estimates than short periods, giving slopes to the curves in Figs. 5 and 6. This was because we assumed $F_{\min}$ and $F_{\max}$ were constant; the longest durations thus create the lowest cumulative F on cohorts present during the increasing-F phase (e.g. Fig. 4 for mackerel) and as noted above, low cumulative F's give the largest errors in estimated abundance. In the Sensitivity Analysis section below, we remove the assumption of a constant $F_{\max}$ and results are similar. Stocks with high M have greater spurious time trends ($|P_S|$) than low M stocks for a given range in cumulative F because errors in abundance estimates for these stocks are inflated more by the larger Z^{VPA} (equation (10)) than estimates for low M stocks.

Similarly, stocks with large M have steeper slopes in Figs. 5 and 6 than stocks with low M (i.e. the former are more sensitive to changes in the duration of the increasing-F phase) because in successive applications of equation (10) in the backwards recursion, the change in errors in N_t resulting from the change in range of cumulative fishing mortality is exaggerated more by the larger Z^{VPA} of large M stocks.

Generalization across stocks

The second purpose of the common F scenarios was to permit generalization of results across stocks. To generalize our findings, we used the variable defined above, $\Delta F\cdot \mathrm{yr}^{-1}\cdot M^{-1}$, which is a measure of the rate of change in intensity of F, relative to M. When the results from the common F scenarios for all stocks were combined, we found an inverse relationship between percent spurious change in recruits and this relative rate of change in intensity of exploitation (outer curves and symbols in Fig. 7). However, the same plot for percent spurious change in biomass (Fig. 8) gave a family of curves; stocks with the lowest M values tended to have smaller percent spurious changes. In

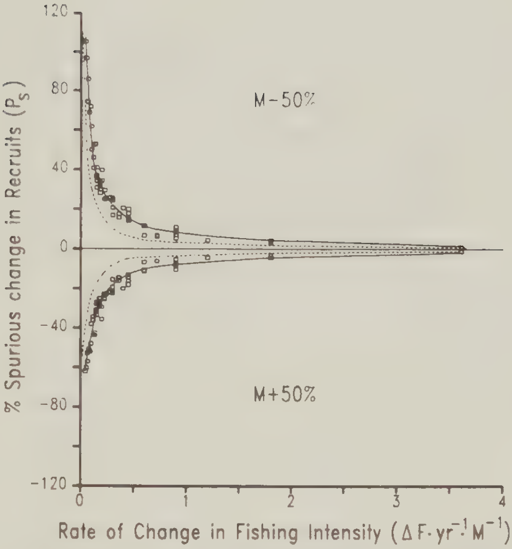


FIG. 7. Percent spurious change in abundance of recruits estimated by VPA in relation to the relative rate of change in fishing intensity (equal to the rate change in F_L per year divided by the true M value for each stock). Top half is for M^{VPA} 50% below M and bottom half is for M^{VPA} 50% above M. Each point in each half represents one stock and one duration of increasing F, with the shortest durations on the right side. Points and outer curves are for F_L ranging from 0.1 to 1.0. Inner dashed curves without points are for F_L ranging from 0.05 to 0.5.

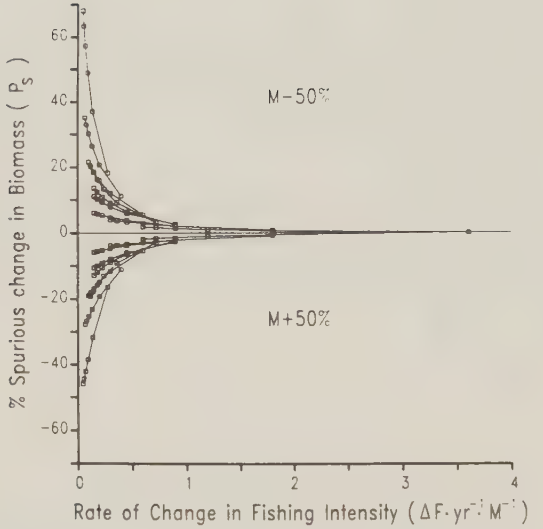


FIG. 8. Same as Fig. 7 except for stock biomass and larger F_l range only. Points of different durations of increasing F are connected for a given stock. Curves for high M stocks have steepest slopes; low M stocks tend to have shallow sloped curves.

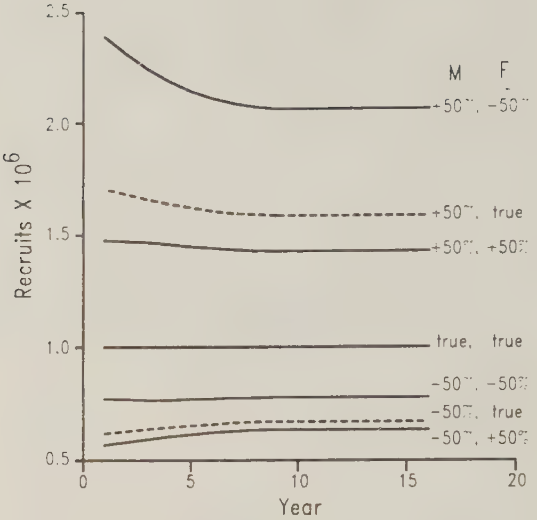


FIG. 9. True recruits (horizontal line) and recruits estimated by VPA under various combinations of errors in M^{VPA} and F_L^{VPA}, for the historical F scenario applied to Dover sole. Dashed curves are for no error in F_L^{VPA} in conjunction with M^{VPA} overestimated (top) or underestimated (bottom) by 50%. Curves for errors in M^{VPA} in conjunction with errors in F_L^{VPA} of ±50% of the true F_L bracket each related dashed curve.

both Figs. 7 and 8, the smallest spurious trends came from cases with rapid increases in F.

Explanation of generalization across stocks

The general patterns in Figs. 7 and 8 result from a combination of processes described in previous sections. We noted above why longer periods of increasing F caused larger absolute values of percent spurious change in abundance estimates. Because long periods of increasing F lead to a slow rate of change in F ($\Delta F \cdot yr^{-1}$) in our common F scenarios, the spurious trends in recruits resulting from an incorrect M^{VPA} are largest at the slowest relative rate of change in fishing intensity (Fig. 7).

Biomass trends for the nine stocks showed a similar qualitative pattern (Fig. 8). Again recall that periods of increasing F cause decreasing trends in true biomass as the older age classes are depleted, and therefore the percent spurious change in biomass is the difference between the true and estimated trends (equation (11)). True percentage decreases in biomass, (P_T), were larger for stocks with low M because, (1) all stocks shared the same F scenarios, (2) F constituted a larger portion of Z for these low M cases than for high M stocks, and (3) stocks with low M therefore experienced relatively greater percentage changes in Z as F increased compared with stocks with high M. However, these large true trends were exaggerated less by VPA in stocks with low M than in stocks with high M because low M stocks have a small Z^{VPA} in equation (10). The net result is that the absolute value of the percent spurious change ($|P_S| = |P_E - P_T|$) is smaller for stocks with lower M. While this is the same qualitative pattern as found for trends in recruitment, biomass trends are also affected by other factors, such as differences in the number of fished ages and the weight-at-age vector, which are not captured by our simple measure of relative rate of change in fishing intensity. This is particularly true at low rates of change in F and it leads to the family of curves in Fig. 8.

Sensitivity Analyses

Changes in assumed F scenarios

We explored the robustness of our results to changes in some of our assumptions. First, we examined how the absolute range in F_L during the increasing F phase influenced our common F scenario results. Previously, we set $F_{min} = 0.1$ and $F_{max} = 1.0$; here we halved that range (0.05 and 0.5) to generate less intensive exploitation. For a given stock, percent spurious changes in recruits were generally smaller for the lower F_L range, and generalized results across stocks and across durations of increasing F were similar to those for the larger F_L range (inner dashed curves in Fig. 7). The smaller range in F_L created smaller differences in cumulative F among successive cohorts, creating smaller spurious time trends than with the large range. These results are distinct from the effect of F_L values on absolute N_t estimates, which become less biased with large cumulative F (Pope 1972).

Second, in the common F scenarios above we assumed a fixed F_{min} and F_{max} and varied the rate of increase in F by changing the number of years of increasing F. In a sensitivity analysis, we simulated an alternative form of F trend where F_{min} was fixed and F_L increased by a fixed amount each year, resulting in a different F_{max} for each duration of the increasing-F period. The results from these runs had the same qualitative pattern as in Figs. 5 and 6; a longer period of increasing F resulted in greater percent spurious change for the same reason as it did in the main results: it generated a wider range in cumulative F values among cohorts than shorter durations.

Changes in assumed errors

In our simplified analyses in previous sections, we assumed that the time series of F_L was known for doing VPA, but if errors were made in that input, the resulting spurious time trends would be different from those we have shown. We therefore added errors in F_L^{VPA} of ±50% of the true F_L. Simultaneous errors in M^{VPA} and F_L^{VPA} either tended to reduce or exaggerate the effects of the error in M^{VPA} alone, depending on the signs of the two errors (e.g. Dover sole in Fig. 9). This was true of both the absolute error in N_t estimates and the percent spurious change for recruits and stock biomass. Trends due to errors in F_L^{VPA} arise through the same mechanisms (differences in cumulative mortality rate among cohorts) noted previously for errors in M^{VPA}. Because errors in M^{VPA} and F_L^{VPA} are unlikely to cancel one another exactly, some spurious time trend will usually result in practice; its magnitude will depend on the relative magnitudes and signs of errors in M^{VPA} and F_L^{VPA}.

We also considered a fixed absolute error in M^{VPA} (e.g. $M \pm 0.1$) rather than a fixed percentage error and again found the same qualitative pattern as in Figs. 5 and 6 of increasing magnitude of spurious change with longer duration of the period of increasing F.

Decreasing recruitments

To simplify our analysis and explanations, we assumed previously that the decreases in stock biomass that occurred as a result of increasing F did not affect recruitment. This was consistent with the marine fish literature, much of which shows that it is very difficult to detect any response of recruitment to changes in spawning stock biomass over the ranges of observed biomasses (reviewed by Rothschild 1986). For our sensitivity analysis, we examined common F scenario situations in which recruitment decreased each year by a given percentage, paralleling the decrease in stock biomass. When compared with the constant recruitment cases presented above, percent spurious time trends that occurred with decreasing recruitment were smaller by at most one-third (for both recruits and biomass) because decreasing trends occurred in both true and estimated abundances. These results were independent of the direction of error in M^{VPA}.

These sensitivity runs clearly show that spurious time trends in abundances reconstructed by VPA are likely to occur under a wide range of conditions when increasing trends in F are present along with an error in one of the parameters input to VPA.

Discussion

Our results show that in the presence of an error in M^{VPA} and an increasing trend in F_L, VPA generates a spurious time trend in both estimated recruits and stock biomass, even if the actual trend in F_L is known. The magnitude of these false trends is greatest when, for a given M and range in F_L, F increases over a long period, that is, when the percentage change in F_L per year is small (Figs. 7 and 8). This counterintuitive result arises because a slow rate of change in F causes relatively low cumulative F on early cohorts and a wider range in cumulative fishing mortality rates than do rapid F increases, and low cumulative F in turn results in more biased abundance estimates for those early cohorts.

We performed our simulations with a time series of F_L values that approximated the trends in F_L observed historically. However, these observed trends in F are affected by the very bias that we document in this paper; most published tables of F estimates for our stocks came from VPA. Thus, the true rate and magnitude of increasing F trends in our historical scenarios may have been over- or underestimated, and the magnitude of the percent spurious changes may be incorrect for those specific scenarios. Nevertheless, the remainder of our conclusions from using the "common F scenarios" are valid; with any time trend in F_L and an error in M^{VPA}, spurious time trends will be embedded in the resulting abundance estimates.

In our simulations, we assumed that increasing trends in F started at the beginning of the time series of the catch data. If we had generated catch data for years prior to the start of an increase in F, and assumed that F was constant at a minimum level during those years, VPA estimates of recruits and biomass would have continued to diverge from the true values (e.g. Fig. 1) as VPA proceeded back through the cohorts until the cumulative fishing mortalities of successive cohorts were identical (i.e. until the cumulative F on recruits reached a constant minimum level off to the left side of Fig. 4.). The estimated abundance for those early years would therefore be constant. Thus, under such conditions, the spurious trends caused by increasing F would be larger than we have reported here. However, for different durations of the increasing-F period, the estimated abundance in the early years would approach the same plateau of constant bias and therefore the same percent spurious change would result. Such a situation could arise in practice if reliable age-specific catch data were available prior to the start of a time trend in F. However, this may be unlikely because the stimulus for starting to gather data often occurs well into the fishing-up phase in development of a fishery. Even if such data were available, spurious time trends would still exist and the effect of M would be as shown previously. The only change from our results above would occur when comparing two identical stocks that had different durations of increasing F, and where data were available for the period prior to the start of the time trend in F. However, our conclusions concerning the effect of different durations of increasing F will hold whenever longer periods of increasing F result in a greater range in cumulative F (e.g. Figs. 5 and 6).

The spurious time trends that we have documented occur in a wider variety of situations than has been shown previously. First, Hilden (1988) documented false time trends in recruitment in the presence of increasing F trends and an error in M, but he made the additional assumption of an underlying stock–recruitment relationship. In our main analysis, we assumed that no change in recruitment occurred over the range of stock biomasses observed during the simulated periods of increasing F, yet we also found spurious trends due to differences in cumulative F among successive cohorts.

Second, the spurious time trends documented by Bradford and Peterman (1989) arose from using catch data in recent years that included incomplete cohorts (year-classes that had not reached the terminal age by the last year of the catch data), and from using "noniterative" VPA, that is, when the partial recruitment vector of age-specific selectivity coefficients was estimated empirically and the VPA was run only once. Analysts use VPA in this way when major changes in catchability have occurred during the period (e.g. Winters et al. 1985). However, we did not include incomplete cohorts in the simulated catch data here and we used the more common "iterative" VPA (Rivard 1983) instead of noniterative VPA. Our spurious trends resulted from a different and more common mechanism (iterative VPA with increasing F trends and an incorrect M^{VPA}) than the trends in Bradford and Peterman (1989) (noniterative VPA with incomplete cohorts and an incorrect M^{VPA} or F_L^{VPA}). Our results are therefore more general than those of Bradford and Peterman (1989) and Hilden (1988) because false trends will occur even if all incomplete cohorts are removed from the input catch data, even if iterative VPA is used, and without any assumed effect of stock biomass on recruitment.

If noniterative VPA is used with catch data sets that include both incomplete cohorts and periods of increasing F, noniterative VPA will either tend to exaggerate the spurious time trend already documented above due to increasing F trends alone, or will result in spurious trends in the opposite direction, again depending on the signs of errors in M^{VPA} and $F_L{}^{\text{VPA}}$ (Bradford and Peterman 1989). Thus, the potential exists for the introduction of complex, nonmonotonic spurious time trends into reconstructed abundances.

We have only addressed increasing F trends but our qualitative results apply more generally to any case in which F tends to increase or decrease (with some variability) over a given period. In the case of a decrease in F, estimates of abundance will converge toward the true value as VPA proceeds back in time through the cohorts, and spurious trends will be opposite in sign from those reported here.

General Implications

These results have considerable relevance for two reasons. First, in practice, M^{VPA} is unlikely to equal the true M. Methods for estimating M for fish populations usually report large confidence intervals (Alverson and Carney 1975; Pauly 1980; Roff 1984; Gunderson and Dygert 1988) or large ranges in different estimates of M for the same species (Vetter 1988), partly because of confounding with other parameters such as the catchability coefficient (Paloheimo 1980). Second, VPA has commonly been used on catch data sets that include periods of increasing F (e.g. references in Table 1 except Fournier (1983) and Archibald et al. (1983)). Thus, the presence of periods of increasing or decreasing trends in fishing mortality rate in past data sets used in VPA may have introduced biases that influenced interpretations of the success or failure of past management actions. As well, studies of mechanisms of variability in recruitment estimated by VPA (e.g. Shepherd et al. 1984; Koslow et al. 1987; Hollowed et al. 1987) and stock–recruitment relations may also have been biased, possibly to the point of masking relationships that were present in nature (Hilden 1988) or creating spurious correlations. Analysts should therefore generate different time series of recruits and stock biomass for each set of parameter estimates used in a VPA. A separate correlation should be performed between the independent variate (such as an environmental factor) and each set of abundance data. Given the natural variability in recruitment and M in nature, and the possibility of time trends in M, it is unlikely that such exercises will identify the true underlying correlations; however, comparisons of results of these different reconstructed time series will demonstrate the sensitivity of such correlations to assumed VPA parameter estimates.

The spurious time trends in abundance estimates caused by increasing F trends may cause problems for some VPA tuning methods, particularly those which use regressions of survey CPUE (catch per unit effort) on VPA estimates (e.g. Rivard 1983; rho method of Pope and Shepherd 1985). Depending on the extent of the F trend bias, the slope from such regressions (i.e. the catchability coefficient) will be biased due to spurious time trends in the estimates from VPA. Therefore, we concur with Mohn (1983) and Pope and Shepherd (1985), who suggest that tuning methods that use effort data are preferable to those that use CPUE data.

Similarly, if spurious time trends in recruitment estimates are present, total allowable catch (TAC) projections will be biased if they are based partly on, (1) projected recruitment from regressions of recruit survey CPUE on VPA recruit estimates (Brander 1987), (2) regressions of VPA recruitment estimates on time (Rivard 1983), or (3) long-term average recruitment (Rivard and Foy 1987). For $M^{\text{VPA}}<M$, projected recruitment and biomass will generally be underestimated, there will be a spurious increasing trend in recruitment, and the estimated decrease in biomass will be less than the true decrease. In contrast, for $M^{\text{VPA}}>M$, projected recruitment and biomass will be overestimated, recruitment will have a spurious decreasing trend, and the estimated decrease in stock biomass will be greater than the true decrease.

The well known problems with VPA have stimulated the development of nonsequential, statistical fitting methods of estimating abundance, which are now gaining wider acceptance as plausible alternatives to VPA (e.g. Doubleday 1976; Fournier and Archibald 1982; Collie and Sissenwine 1983; Deriso et al. 1985; Gudmundsson 1986; Methot 1989). These methods may be more robust to errors in input parameters, particularly F_L, because they commonly use auxilliary data to help determine estimates. However, most fitting methods require as input an assumed and constant M value and for those which permit estimation of M, M estimates are poorly determined (e.g. Fournier 1983) and very sensitive to errors in other inputs (e.g. aging errors; Fournier and Archibald 1982). Thus, while it is clear that nonsequential techniques will produce biased abundance estimates when M is incorrect, it is not clear whether errors in input parameters will lead to spurious time trends in estimates obtained from such techniques. Therefore, analysts must determine how sensitive abundances estimated by the new fitting methods are to errors in input information. The history of VPA work clearly demonstrates the necessity of such sensitivity analyses; in recent years, analytical and numerical analysis techniques have shown that under certain commonly found circumstances, VPA outputs are quite sensitive to errors in inputs and assumptions (e.g. Ulltang 1977; Sims 1984; Rivard and Foy 1987; Sampson 1987; 1988; Kimura 1989; Bradford and Peterman 1989). These same techniques should be used in rigorous evaluations of the new statistical fitting methods that some researchers hope will replace VPA. Some evaluations have been done (e.g. Deriso et al. 1989) but they should also include cases in which trends in F occur.

Regardless of which stock reconstruction method analysts use, our results and others noted above emphasize the importance of presenting to fishery managers the results of sensitivity analyses when parameters are uncertain. Such information is essential to enable managers to make the best possible decisions, given the large uncertainty in our understanding of these systems. As well, it is essential that more effort be directed at obtaining more precise and accurate estimates of data used in analyses, especially key parameters such as M, because no stock reconstruction method can completely avoid bias if parameter estimates are poor.

Acknowledgments

Michael Bradford, Jeremy Collie, and three anonymous reviewers as well as Geoff Evans, made useful suggestions on a draft manuscript. Funding was provided by an operating grant to R. M. Peterman from the Natural Sciences and Engineering Research Council of Canada and a Special Research Projects Grant from Simon Fraser University.

References

Agger, P., I. Boetius, and M. Lassen. 1973. Error in the virtual population analysis: the effect of uncertainties in the natural mortality coefficient. J Cons. Int. Explor. Mer 35: 93.

Alverson, D. L. and M. J. Carney. 1975. A graphical review of the growth and decay of population cohorts. J. Cons. Int. Explor. Mer 36: 133–143

Anderson, E. D., and A. J. Paciorkowski. 1980. A review of the northwest Atlantic mackerel fishery. Rapp. P.-V. Reun. Int. Explor. Mer 177: 175–211.

Archibald, C. P., D. Fournier, and B. M. Leaman. 1983. Reconstruction of stock history and development of rehabilitation strategies for Pacific ocean perch in Queen Charlotte Sound, Canada. N. Am. J. Fish. Manage. 3: 283–294.

Arenholz, D. W., W. R. Nelson, and S. P. Epperly. 1987. Population and fishery characteristics of Atlantic menhaden, (*Brevoortia tyrannus*). Fish. Bull. 85: 569–600.

Bradford, M. J., and R. M. Peterman. 1989. Incorrect parameter values used in virtual population analysis (VPA) generate spurious time trends in reconstructed abundances. *In* R. J. Beamish and G. A. McFarlane [ed.] Effects of ocean variability on recruitment and on evaluation of parameters used in stock assessment. Can. Spec. Publ. Fish. Aquat. Sci. 108 (In press)

Brander, K. 1987. How well do working groups predict catches? J. Cons. Int. Explor. Mer 43: 245–252.

Collie, J. S., and M. P. Sissenwine. 1983. Estimating population size from relative abundance data measured with error. Can. J. Fish. Aquat. Sci. 40: 1871–1879.

Deriso, R. B., P. R. Neal, and T. J. Quinn II. 1989. Further aspects of catch-age analysis with auxiliary information. *In* R. J. Beamish and G. A. McFarlane [ed.] Effects of ocean variability on recruitment and on evaluation of parameters used in stock assessment. Can. Spec. Publ. Fish. Aquat. Sci. 108 (In press)

Deriso, R. B., T. J. Quinn II, and P. R. Neal. 1985. Catch-age analysis with auxiliary information. Can. J. Fish. Aquat. Sci. 42: 815–824.

Doubleday, W. G. 1976. A least squares approach to analyzing catch at age data. Int. Comm. Northw. Atlant. Fish. Res. Bull. 12: 69–81.

Espino, M. A., and C. Wosnitza-Mendo. 1986. Peruvian hake fisheries from 1971 to 1982. Calif. Coop. Oceanic Fish. Invest. Rep. 27: 113–120.

Fournier, D. A. 1983. An analysis of the Hecate Strait Pacific cod fishery using an age-structured model incorporating density-dependent effects. Can. J. Fish. Aquat. Sci. 40: 1233–1243.

Fournier, D. A., and C. P. Archibald. 1982. A general theory for analyzing catch at age data. Can. J. Fish. Aquat. Sci. 39: 1195–1207.

Francis, R. 1986. Two fisheries biology problems in west coast groundfish management. N. Am. J. Fish. Manage. 6: 453–462.

Gulland, J. A. 1983. Fish stock assessment. Wiley-Interscience. Chichester, U.K. 223 p.

Gunderson, D. R., and P. H. Dygert. 1988. Reproductive effort as a predictor of natural mortality rate. J. Cons. Int. Explor. Mer 44: 200–209.

Gudmundsson, G. 1986. Statistical considerations in the analysis of catch-at-age observations. J. Cons. Int. Explor. Mer 43: 83–90.

Hayman, R. A., A. V. Tyler, and R. L. Demory. 1980. A comparison of cohort analysis and catch per unit effort for Dover sole and English sole. Trans. Am. Fish. Soc. 109: 35–53.

Hightower, J. E., and G. D. Grossman. 1985. Comparison of constant effort harvest policies for fish stocks with variable recruitment. Can. J. Fish. Aquat. Sci. 42: 982–988.

Hilden, M. 1988. Errors of perception in stock and recruitment studies due to wrong choices of natural mortality rate in virtual population analysis. J. Cons. Int. Explor. Mer 44: 123–134.

Hoag, S. H., and R. S. McNaughton. 1978. Abundance and fishing mortality of Pacific halibut, cohort analysis, 1935–1976. Int. Pac. Halibut Comm. Sci. Rep. 65, 45 p.

Hollowed, A. B., K. M. Bailey, W. S. Wooster. 1987. Patterns in recruitment of marine fishes in the northeast Pacific Ocean. Biol. Oceanogr. 5: 99–131.

IMSL. (International Mathematical and Statistical Library). 1982. International mathematical and statistical library reference manual. IMSL, Houston, TX.

Kimura, D. K. 1989. Variability in estimating catch-in-numbers-at-age and its impact on cohort analysis. *In* R. J. Beamish and G. A. McFarlane [ed.] Effects of ocean variability on recruitment and on evaluation of parameters used in stock assessment. Can. Spec. Publ. Fish. Aquat. Sci. 108 (In press)

Koslow, J. A., K. R. Thompson, and W. Silvert. 1987. Recruitment to northwest Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) stocks: influence of stock size and climate. Calif. Coop. Oceanic Fish. Invest. Rep. 18: 136–148.

MacCall, A. D. 1976. Density dependence of catchability coefficient in the California Pacific sardine, *Sardinops sagax caerula*, purse seine fishery. Calif Coop. Oceanic Fish. Invest. Rep. 18: 136–148.

1986. Virtual population analysis (VPA) equations for nonhomogeneous populations, and a family of approximations including improvements on Pope's cohort analysis. Can. J. Fish. Aquat. Sci. 43: 2406–2409.

Methot, R. D. 1989. Synthetic estimates of historical abundance and mortality for northern anchovy, *Engraulis mordax*. *In* E. F. Edwards and B. A. Megrey [ed.] Mathematical analysis of fish stock dynamics: reviews, evaluations and current applications. Am. Fish. Soc. Symp. Ser. No. 6. American Fisheries Society, Bethesda, MD. (In press)

Mohn, R. K. 1983. Effects of error in catch and effort data on tuning cohort analysis, with a postscript on logistic production models, p. 141–150. *In* W. G. Doubleday and D. Rivard [ed.] Sampling commercial catches of marine fish and invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 66.

Muller, D. E. 1956. A method for solving algebraic equations using an automatic computer. Mathematical Tables and Other Aids to Computation 10: 208–215.

Murphy, G. I. 1965. A solution of the catch equation. J. Fish. Res. Board Can. 22(1): 191–202.

Paloheimo, J. E. 1980. Estimation of mortality rates. Trans. Am. Fish. Soc. 109: 378–386.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer 36: 175–192.

Pope, J. G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. Int. Comm. Northw. Atlant. Fish. Res. Bull. 9: 65–74.

Pope, J. G., and D. Gray. 1983. An investigation of the relationship between the precision of assessment data and the precision of total allowable catches, p. 151–157. *In* W. G. Doubleday and D. Rivard [ed.] Sampling commercial catches of marine fish and invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 66.

Pope, J. G., and J. G. Shepherd. 1985. A comparison of the performance of various methods for tuning VPAs using effort data. J. Cons. Int. Explor. Mer 42: 129–151.

Prager, M. H., and A. D. MacCall. 1988. Sensitivities and variances of virtual population analysis as applied to the mackerel, *Scomber japonicus*. Can. J. Fish. Aquat. Sci. 45: 539–547.

Ricker, W. E. 1973. Two mechanisms that make it possible to maintain peak-period yields from stocks of Pacific salmon and other fishes. J. Fish. Res. Board Can. 30: 1275–1286

1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can. Bull. 191: 382 p.

Rivard, D. 1983. Effects of systematic, analytical, and sampling errors on catch estimates: a sensitivity analysis, p. 114–129. *In* W. G. Doubleday and D. Rivard [ed.] Sampling commercial catches of marine fish and invertebrates. Can Spec. Publ. Fish. Aquat. Sci. 66.

Rivard, D., and M. G. Foy. 1987. An analysis of errors in catch projections for Canadian Atlantic fish stocks. Can. J. Fish. Aquat. Sci. 44: 967–981.

Roff, D. A. 1984. The evolution of life history parameters in teleosts. Can. J. Fish. Aquat. Sci. 41: 989–1000.

Rothschild, B. J. 1986. Dynamics of marine fish populations. Harvard University Press, Boston, 277 p.

Sampson, D. B. 1987. Variance estimators for virtual population analysis. J. Cons. Int. Explor. Mer 43: 149–158.

1988. The stability of virtual population analysis cohort size estimates. J. Cons. Int. Explor. Mer 44: 135–142.

Saville, A., and R. S. Bailey. 1980. The assessment and management of the herring stocks in the North Sea and to the west of Scotland. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 177: 112–142.

Shepherd, J. G., J. G. Pope, and R. D. Cousens. 1984. Variations in fish stocks and hypotheses concerning their links with climate. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 185: 255–267.

Sims, S. E. 1984. An analysis of the effect of errors in the natural mortality rate on stock-size estimates using virtual population analysis (cohort analysis). J. Cons. Int. Explor. Mer 41: 149–153.

Ulltang, O. 1976. Catch per unit of effort in the Norwegian purse seine fishery for Atlanto–Scandinavian herring. FAO Fish. Tech. Pap. 155: 91–101.

1977. Sources of errors in and limitations of virtual population analysis (cohort analysis). J. Cons. Int. Explor. Mer 37: 249–260.

Vetter, E. F. 1988. Estimation of natural mortality in fish stocks: a review. Fish. Bull. 86: 25–42.

Wakabayashi, K. 1984. Estimations of biomass and yield for yellowfin sole in the eastern Bering Sea. Int. North. Pac. Fish. Comm. 42: 65–72.

Winters, G. M., E. L. Dalley, and J. A. Moores. 1985. Fortuity disguised as fisheries management: the case history of Fortune Bay herring. Can. J. Fish. Aquat. Sci. 42 (Suppl. 1): 263–274.

8934

5.2. Applications de la télédétection satellitaire du germon du Pacifique Nord , *Thunnus alalunga (Bonnaterre)*

R. Michaël LAURS
South West Fisheries Center,
National Marine Fisheries Service, NOAA
La Jolla, C.A. 92038 (USA)

Introduction

Durant les années récentes, la télédétection satellitaire est demeurée une source importante d'information océanographique utilisée par les biologistes et océanographes des pêcheries dans le domaine des recherches sur le germon et par les pêcheurs U.S. pour le développement des stratégies de pêche au germon dans le Pacifique Nord. Il n'est pas possible d'utiliser les satellites pour détecter directement les bancs de germon ni de mesurer ou collecter à partir de l'espace le spectre complet d'information nécessaire pour apprécier les

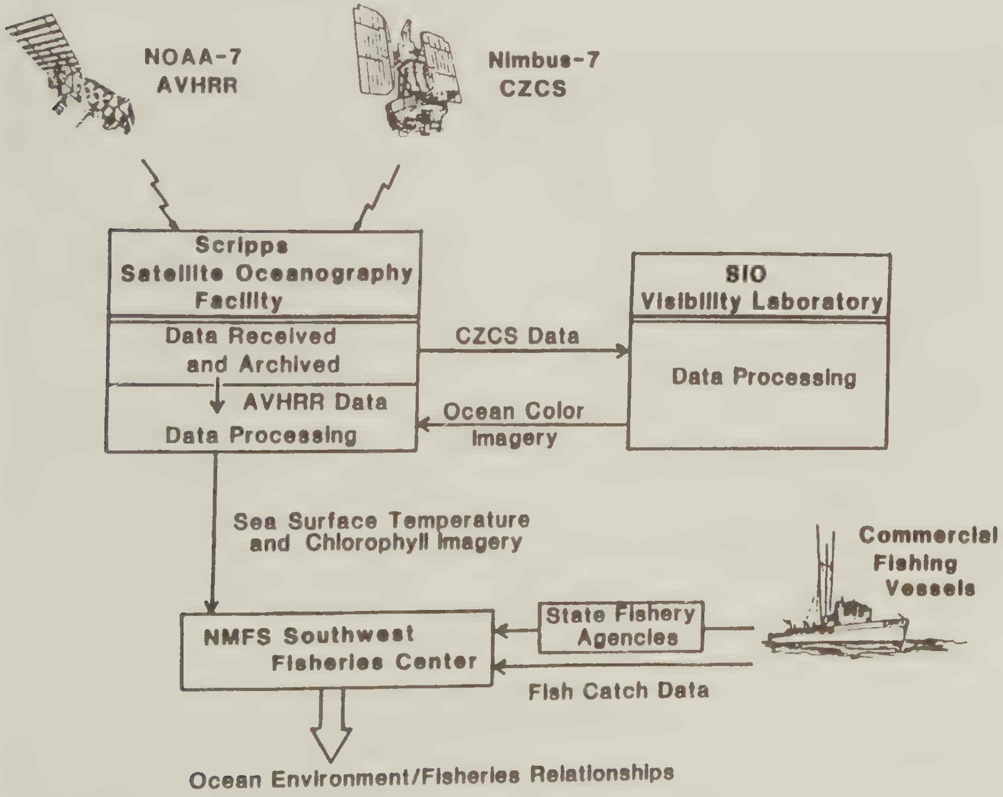


Figure 1 - Reseau de collecte et traitement des données utilisé par le National Marine Fisheries Service, South West Fisheries Center sur la cote ouest des USA (adapte de Laurs *et al.*, 1984)

modifications de l'environnement marin qui affectent le germon. Néanmoins les processus océanographiques clés et les conditions qui peuvent influencer la distribution, la disponibilité et la vulnérabilité du germon peuvent être déduits des mesures faites à partir des satellites, comme par exemple les limites des fronts océaniques, les grandes structures des courants et de la circulation océanique, les remontées d'eau (up-welling) côtières, la concentration en pigment chlorophyllien, la distribution de la température de surface (SST). Les mesures de température superficielle obtenues à partir des relevées infra-rouges par les satellites défilants à orbite polaire NOAA, les mesures de la couleur de l'océan par le scanner couleur en zone côtière (CZCS) du satellite NIMBUS-7 ont été largement utilisés en relation avec la connaissance et l'exploitation du germon du Pacifique Nord. De plus, les mesures de champs de vent faites par le dispersiomètre de SEASAT ont été récemment utilisées dans des analyses de pêcheries incluant le germon de cette zone.

Application de la télédétection satellitaire à la recherche sur le germon du Pacifique Nord

La télédétection satellitaire a démontré sa qualité en tant qu'outil pour la recherche sur le germon du Pacifique Nord. Ceci a été particulièrement vrai dans les études dévolues à la distribution, la capturabilité et la vulnérabilité en relation avec les conditions et les processus océanographiques.

Laurs *et al.* (1984) ont démontré que les caractéristiques environnementales appréciées par l'infrarouge et les images en couleur de la surface de la mer définissent les frontières pour les aggrégations de germon et les zones de pêche telles qu'elles apparaissent par les enregistrements de pêche commerciale. Cette étude a été menée grâce à un réseau concourant d'information et de données satellitaires et de pêche. Ce réseau, dont un schéma est donné à la figure 1, nécessite la coopération entre le chercheur sur les pêcheries, des agences fédérales et des états, les structures de réception et de traitement des donnees satellitaires, et l'industrie germonière U.S.

La radiométrie AVHRR à haute résolution et le scanner CZCS pour la couleur des zones côtières, sont reçus directement des satellites NOAA-7 et NIMBUS-7, respectivement à la Scripps Institution of Oceanography Satellite Oceanography Facility (SSOF). Les données du satellite lors de son passage au-dessus des eaux côtières au large de la Californie, et couvrant une région au large des états Oregon et Washington (Figure 2), ont été obtenues durant les périodes de pêche intensive par la flottille germonière U.S.

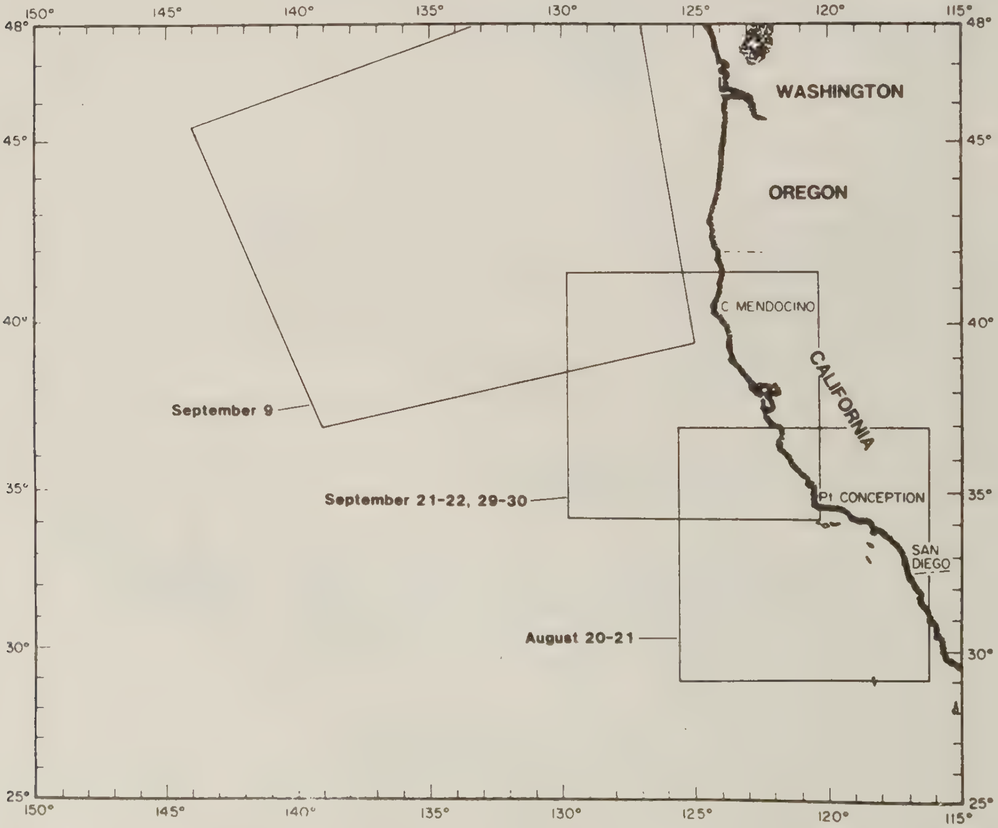


Figure 2 : Localisation des images pour la recherche de la distribution des captures en relation avec les caractéristiques de l'environnement observées à partir des satellites (from Laurs *et al.*, 1984).

Les valeurs de radiance du canal 4 (10.5 a 11.3 nannometres) et du canal 5 (11.5 a 12.5 nannometres) sont converties en valeur de temperature en utilisant une calibration disponible a la SSOF, developpee par Lauritson *et al* (1979). Les temperatures de surface SST corrigees des effets atmospheriques, sont estimees en utilisant un algorithme multi-canaux developpe par Mc Clain *et al* (1983). Les images de temperature de surface SST sont recalees par des points de reference au sol de telle façon que les images de SST et de couleur soient identiques.

Les radiances de la bande 1 (blanc) et de la bande 3 (verte) issues du CZCS sont corrigees de l'effet Rayleigh et de la dispersion sur l'aerosol par un algorithme atmospherique, modifie par Smith et Wilson (1981), d'une version produite par l'equipe experimentale de CZCS de NIMBUS. Le rapport bleu/vert est converti en indice de concentration phytoplanctonique en utilisant un algorithme pigmentaire dû a Clark (1981). Les dimensions des pixels des images cotieres et du large de CZCS sont de 1,6 et 2,4 km respectivement.

Les donnees de capture de germon sont obtenues a partir des carnets de peche quotidiens fournis volontairement par les pecheurs. Les positions ont le plus souvent ete enregistrees au debut de chaque journee de peche, qui se developpe sur pres de 50 km. Les captures sont standardisees pour un effort de 150 heures de ligne, representant une journee de peche standard d'un ligneur americain. Les captures par unite d'effort (C.P.U.E.) pour des periodes de deux journees precedent a deux journees suivant le passage du satellite ont ete reparties sur les images de temperature et de teneur en pigment pour les zones cotieres. Les donnees de capture pour les zones au large ont ete moyennees par carre de 1° pour une periode de 15 jours et reportees sur les images satellitaires.

Les images satellitaires et les captures donnees de peche concourantes (Figures 3 a 10) montrent clairement que les images thermiques infra-rouge et les donnees de couleur dans le visible, permettent de definir les limites environnementales de la distribution spatiale des aggregations de germon, de façon plus efficace que ne le permettent les observations a partir de navires ou d'avion. L'etude demontre de façon convaincante que la distribution et la disponibilite du germon

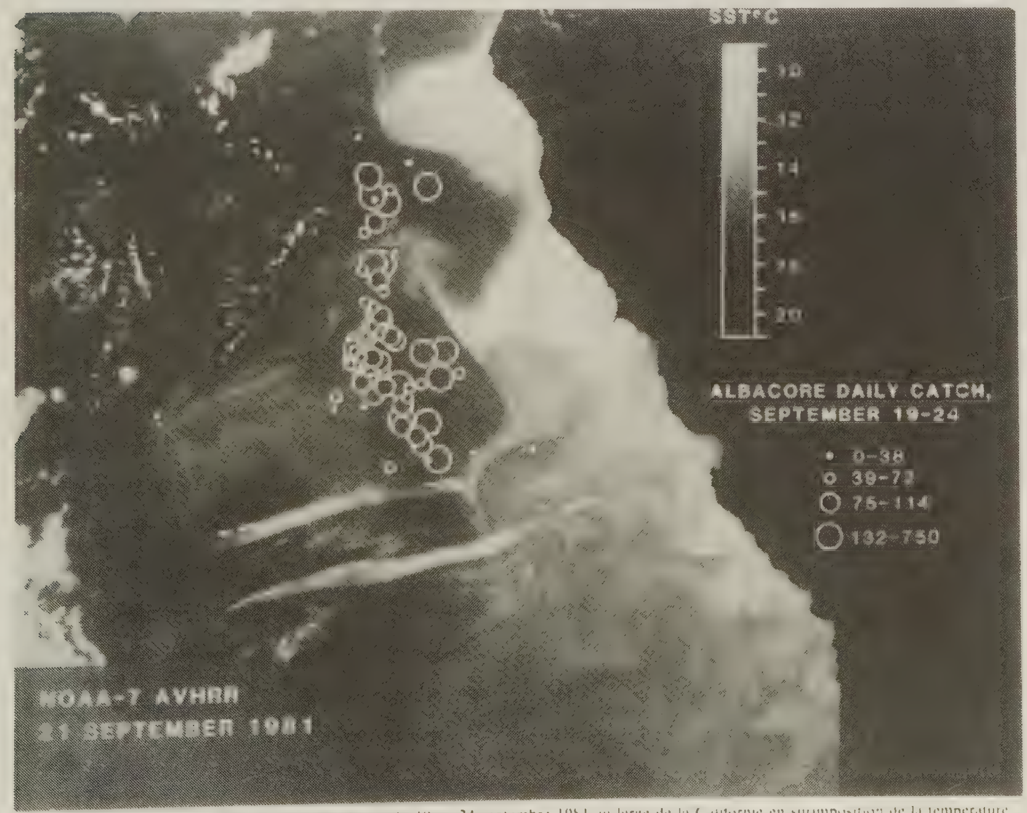


Figure 3 - Captures quotidiennes de germon realisees du 19 au 24 septembre 1981 au large de la Californie en surimposition de la temperature de surface issues des donnees satellitaires du 22 septembre 1981 1040 3PST (adapte de Laurs *et al* 1984).

au large de la côte ouest des U.S.A. sont directement reliees aux fronts oceaniques associes aux remontees dues aux up-wellings côtiers (Figures 3 a 8). Les concentrations de germon exploitables commercialement sont situees dans les eaux chaudes, les eaux oceaniques bleues situees pres des fronts thermiques et colores sur la bordure a la côte des masses oceaniques. Des fronts relativement intenses sont tres propices et les intrusions, en direction de la côte, d'eau océanique chaude claire particulierement favorables a la presence de bancs de germons.

L'etude montre aussi que dans des masses d'eau situées à des centaines de milles au large à la fin de l'ete, des concentrations commerciales de germon sont associees à des zones frontales oceaniques detectables à partir des images « couleurs » satellitaires, sans gradient thermique.

La disponibilité de germon dans les eaux du large semble plus élevée dans des eaux de relativement plus forte production. Laurs et Lynn (1977) ont montré que la migration du germon dans les eaux côtieres nord-américaines est associée à la zone de transition du Pacifique Nord et ses zones frontales, qui montrent de tres forts gradients thermiques SST durant les mois de printemps. Le rechauffement saisonnier et la diminution de mélange par le vent, sans aucun doute, joue un rôle dans l'absence totale de gradient thermique associé au front de couleurs à la fin de l'ete.

La distribution du germon durant l'hiver dans les zones situées à quelques centaines de milles au large de la côte américaine ouest est aussi reliée aux fronts thermiques, qui paraissent marquer la frontière extérieure du Courant de Californie, observees par l'imagerie AVHRR (Laurs *et al.*, 1981).

Jurick (1985) a étudié les relations entre les captures commerciales de germon et les analyses de frontiere thermique distribuées aux pêcheurs américains. Son étude portait sur les mois de juillet jusqu'à octobre pour les années 1976 à 1978. Il utiliait des données de captures obtenues à partir des carnets de pêche (Laurs *et al.*, 1975), standardisées selon la méthode exposée par Laurs *et al.* (1976), et moyennées pour donner une capture moyenne par jour et par bateau pour un carré de 1°. Une information supplémentaire sur le rendement de la pêche au germon est obtenue à partir des bulletins sur la pêche au germon produits par quinzaine par le National Marine Fisheries Service (NMFS) (Laurs, 1977). Les cartes d'analyse des zones frontales, qui etaient obtenues sur une base hebdomadaire, sont produites à partir de l'imagerie VHRR telle que décrite par Breaker (1981) et distribuees par la NOAA/National Environmental Satellite Service.

Jurick (1985) a montré que dans 70 % des cas, les captures etaient plus fortes dans les quadrangles contenant une ou plusieurs zones frontales/frontieres définies par l'imagerie satellite que dans les autres quadrangles. Les plus fortes captures en moyenne sont situees à 70 % dans les quadrangles contenant de larges frontières thermiques, 33 % dans les quadrangles à faible frontière thermique, 25 % dans les quadrangles à forte frontiere thermique.

Jurick considère que les plus fortes captures sont plus souvent associées aux larges frontieres thermiques qu'aux fortes frontieres thermiques en raison du laps de temps necessaire, apres le developpement d'une nouvelle forte zone frontale, pour l'aggregation des organismes fourrage devant conduire a une zone favorable d'alimentation du germon.

Par ailleurs, Jurick a montré que 83 % des zones les plus productrices durant les saisons de pêche au germon etudiees etaient associées a des structures thermiques decrites dans les analyses de zone frontière : 48 % des cas se produisirent après que des cartes aient ete distribuees, et pourraient avoir ète preditées à partir des cartes distribuees. Finalement, l'analyse statistique a montre que 7 des 8 periodes testees ont montre une localisation de zone de pêche significativement plus efficace lorsqu'il y a eu utilisation des zones thermiques frontieres. Jurick conclut que les zones frontières thermiques deduites de l'analyse satellitaire constituent un outil de haute qualite pour l'identification des aires de pêcherie potentielle de germon.

Svejkovsky (1988) a utilisé l'imagerie satellitaire NOAA AVHRR et les donnees de CPUE de germon pour analyser les causes possibles d'aggregation au large de la Californie. Le traitement d'image satellitaire a ete utilisé par Svejkovsky pour estimer les caracteristiques thermiques superficielles et les taux de dissipation ou d'intensification des fronts thermiques. En pratique, une serie d'images AVHRR portant généralement sur 6 à 7 jours ont été calibrees, lissées à l'aide d'un filtre a moyenne mobile, rectifiées géométriquement, et dépouillées de l'influence des nuages par l'application d'un masque spécifique. Une approximation dérivee spatiale a eté calculée pour chaque image et l'image « gradient » résultant filtree pour en éliminer tous les gradients de valeur inférieure à 0,1°/km. En utilisant ces procédures Svejkovsky a pu analyser qualitativement et quantitativement les fronts thermiques superficiels SST, et en notant les changements des structures frontales sur les images successives, décrire les variations des positions et de l'intensité des zones frontales dans le temps et l'espace.

Les variations dans le succès des pêches au germon ont été analysées par Svejkovsky (1988) à partir des carnets de pêche (Laurs *et al.*, 1975). Les données de pêche ont été standardisées en valeurs de rendement (CPUE) journaliers exprimés comme le nombre de germons capturés pour 150 heures de ligneur par degre de 1°. Les moyennes des rendements CPUE pour 7 jours ont été calculées pour chaque quadrangle de 1° latitude/longitude au large de la Californie pour les saisons de pêche au germon de 1980 à 1983.

L'examen de ces valeurs de rendement de pêche (CPUE) montre l'existence de différents types ou situations reliées aux variations dans la structure du front océanique telle qu'elle peut être appréciée à l'aide du radiomètre AVHRR. La plupart des zones pêchées montrent de fréquentes fluctuations du rendement de pêche autour de la moyenne. Occasionnellement, une zone peut montrer un accroissement abrupt des captures qui sera suivi par un effondrement également brusque. Ce dernier type de comportement a été associé a une présence stable et persistante des fronts thermiques. Les bonnes pêches semblent maintenues stables dans ces zones jusqu'à plusieurs semaines, puis peuvent tomber très rapidement si les frontières thermiques sont détruites par un changement du régime des vents. Ces résultats corroborent ceux obtenus par les marquages acoustiques et suivis des germons (Laurs *et al.*, 1976) qui ont montré que les germons demeurent à proximité des frontières associées aux up-welling au large de la Californie centrale, mais migrent très rapidement au large de cette zone quand cette frontière est détruite par des changements ou translations du régime des vents, changements défavorables à l'installation de remontées d'eau profondes.

Svejkovsky a également montré que les bons rendements de pêche ne sont pas toujours associés aux zones à fort gradient thermique. Ceci est particulièrement évident quand les structures frontales persistantes bien établies, sont remplacées par des frontières nouvelles intenses formées par des modifications du régime des vents. Les rendements CPUE sont réduits de 50 % ou plus de ce qu'ils étaient avant la rupture et destruction de l'ancienne structure, bien que des structures thermiques fortes nouvelles soient formées par le nouveau régime et exploitées intensément par la flottille.

Svejkovsky suppose que les conditions nécessaires à l'établissement d'un environnement favorable (alimentaire notamment) à la concentration du germon peuvent être réalisées à proximité de structures thermiques stables persistantes, mais pas dans les zones où un front vient d'être récemment établi. Son etude démontre clairement que des modifications soudaines dans l'agrégation des germons sont révélatrices de processus dynamiques ayant affecté la stabilité de structures frontales dans la température de surface.

Laurs (en préparation) a utilisé des images AVHRR et CZCS en conjection avec le marquage acoustique et des observations océanographiques concourantes pour analyser les mécanismes possibles responsables de l'agrégation du germon à proximité des frontières des up-welling côtiers. Il apparait que l'agrégation des germons dans la rive chaude, océanique claire des up-welling et l'évitement des zones d'eaux à haute productivité et haute densité de proies sur la rive gauche, turbide, ascensionnelle par les germons est déterminée par la clarté de l'eau. Les résultats suggèrent que la clarté de l'eau détermine la possibilité et la capacité de vision et détection des proies, plus que les conditions thermiques, et constitue le facteur environnemental déterminant la distribution du germon dans les zones d'up-welling côtiers.

Un cas d'étude des variations du rendement de la

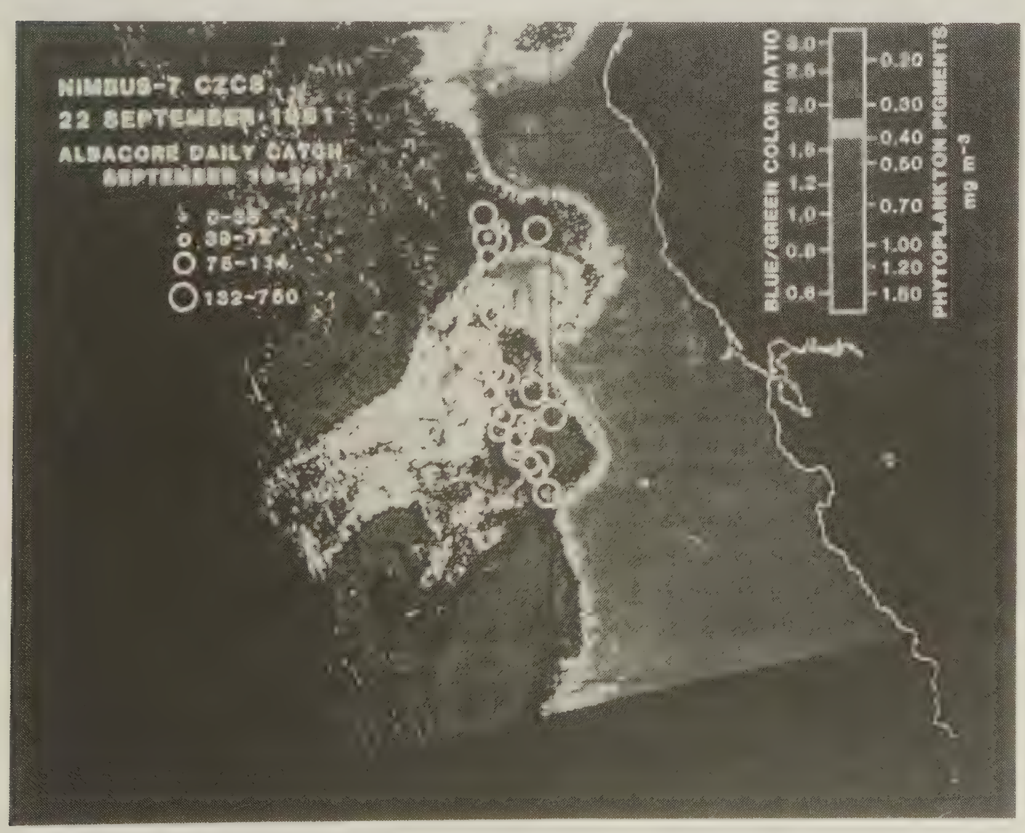


Figure 4 : Captures quotidiennes de germon du 19 au 24 septembre 1981 au large de la Californie en surimposition des images du CZCS de NIMBUS-7; rapport bleu/vert et indice de concentration phytoplanctonique, 22 septembre 1981, 1104 PST (adapté de Laurs *et al.*, 1984)

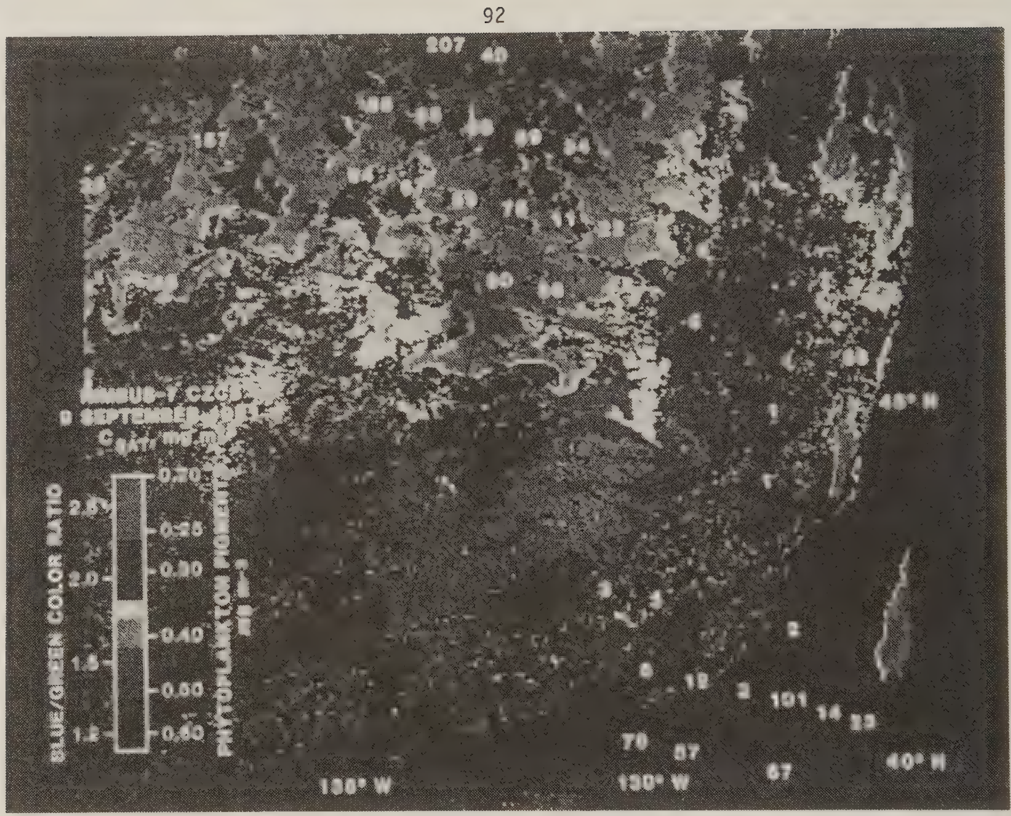


Figure 5 : Captures moyennes quotidiennes de germon par carre de 1° du 1 au 15 septembre 1981 en surimposition des images du CZCS de NIMBUS-7 : rapport bleu/vert et indice de concentration phytoplanctonique, 9 septembre 1981, 1215 PST (adapte de Laurs *et al.*, 1984)

pêche nord-americaine au germon et de son habitat en liaison avec les caracteristiques oceanographiques et hydro-climatiques mesurees par les capteurs satellitaires : infra-rouge, dispersiometre, alimetre est en cours de progres par Laurs, Svejkovsky et Hess (en cours). Cette etude est en cours de realisation pour evaluer l'interêt des mesures realisees par les capteurs actifs (altimetriques, dispersiometriques) sur l'etat de surface de la mer et des champs de vent, en addition des mesures infra-rouges de la temperature de la mer, pour detecter et mesurer en permanence les conditions oceanographiques qui affectent l'écologie et la pêche du germon. Cette information est particulierement abondante, volumineuse et importante, en raison du fait qu'un enorme volume de donnees de ce type deviendront disponibles en routine sur l'ensemble de l'ocean mondial avec le lancement de nombreux vecteurs et capteurs meteorologiques actifs durant la decade a venir. Les donnees resultantes devraient apporter d'enormes capacites de mesure et de surveillance des caracteristiques de l'environnement marin qui jouent un rôle determinant dans la repartition, les migrations et les conditions de peche de poissons hautement migratoires. Les donnees des dispersiometres et des altimetres peuvent être particulierement utiles dans les parties centrales des oceans ou l'information oceanographique est generalement manquante sur la base spatiale et temporelle necessaire pour la recherche et les applications a la pêche.

L'etude utilise les donnees du dispersiometre (SASS) et de l'altimetre du satellite SEASAT et des images infra-rouges VHRR de NOAA5, et les donnees de pêche (CPUE) du germon de la même periode. Les resultats preliminaires montrent une bonne correspondance entre la pêche au germon et les types de convergence et divergence oceaniques issus du dispersiometre SASS, notamment l'intensité des champs de vent moyennees sur des periodes de 7 jours.

Application de la télédétection satellitaire à l'exploitation du germon du Pacifique Nord par les pêcheurs americains U.S.

Les pêcheurs U.S. de germon utilisent largement les produits issus de l'imagerie satellitaire pour determiner les zones favorables a la concentration des poissons et pour la securite des navires. Ils ont ete parmi les premiers pecheurs a reconnaitre l'interêt de la teledetec-

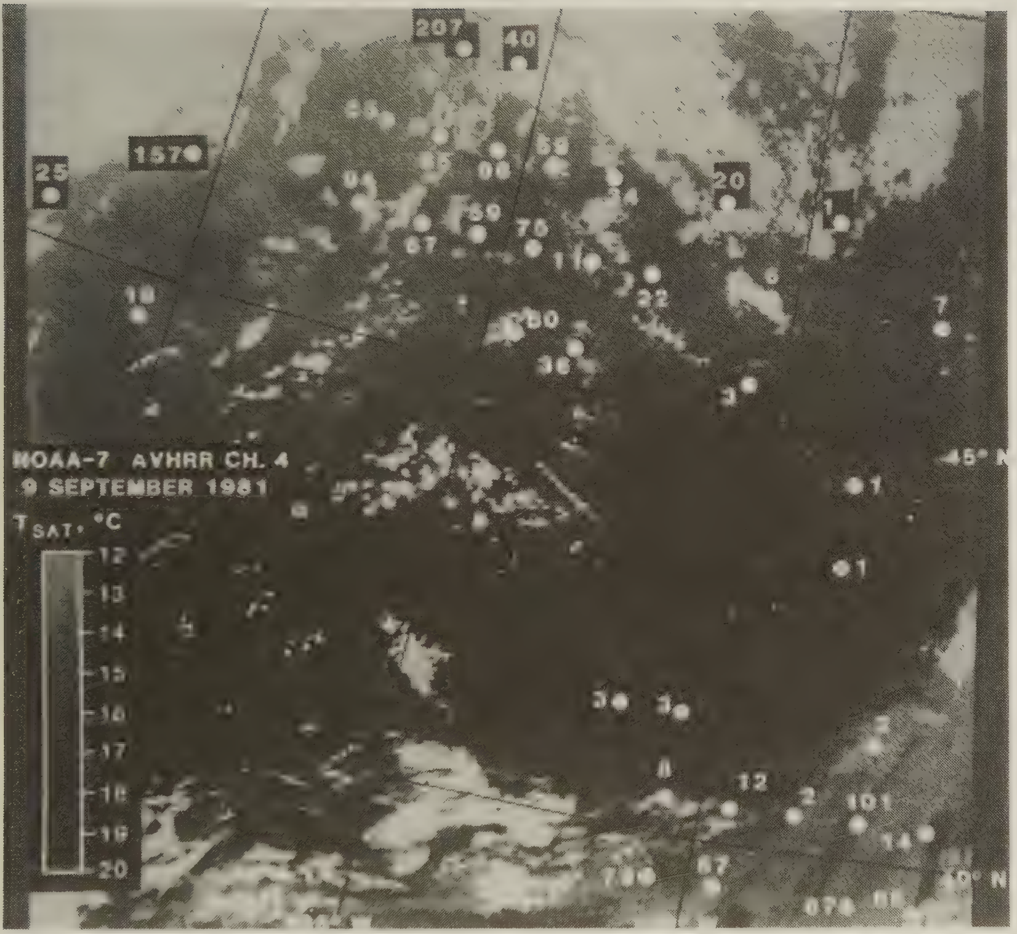


Figure 6 : Captures moyennes quotidiennes de germon par carre 1° du 1 au 15 septembre 1981 en surimposition de la temperature de surface du 9 septembre 1981, 1438 PST (adapte de Laurs *et al.*, 1984)

tion satellitaire pour les pêcheries. Ils ont egalement ete tres cooperatifs pour l'utilisation de la nouvelle technologie satellitaire et de ses produits lorsque ceux-ci ont eté rendus disponibles.

Les premières informations et donnees satellitaires ont été utilisées pour la premiere fois pour l'aide à la pêche par les pêcheurs americains dans les premieres annees 1970. Cette premiere tentative utilisait les images du domaine visible et infra-rouge reçues par le systeme APT (Automatic Picture Transmission), en conjonction avec d'autres donnees pour preparer les cartes d'aide à la pêche transmises par radio-fac simile aux thoniers senneurs US operant dans l'Ocean Pacifique Tropical Est (Laurs, 1971). Une revue de l'utilisation des donnees satellites pour l'élaboration d'elements d'aide à la pêche au germon pour les pêcheurs americains et d'autres nationalites sont disponibles dans les travaux de Fiedler *et al.* (1985), Laurs et Bruscks (1985), Njoku *et al.* (1985) et Montgomery *et al.* (1986). Les analyses routinieres de temperature de surface a partir de donnees satellitaires ont été produites pour les eaux cotieres au large de la côte ouest des U.S.A., depuis 1976 (Breaker and Jurick, 1975). Le format, degre de detail et methodes de dissemination de ces analyses, sous forme de cartes, ont varie au cours des annees. Breaker (1981) a decrit les methodes utilisees pour preparer ces cartes et Short (1979) a donne une information sur l'utilisation de ces cartes par les pêcheurs. Un exemple de la forme actuelle de l'analyse de la temperature de surface de la mer est donne dans la figure 8. Les frontieres thermiques sont obtenues a partir des donnees de l'AVHRR et les isothermes sont essentiellement fondes sur des observations *in situ* produites par les navires et les bouees. Ces cartes sont produites deux fois par semaine et distribuees aux pêcheurs par radio-fac-simile et par courrier

Il existe egalement une analyse des frontieres thermiques de temperature superficielle de la mer a partir des donnees AVHRR avec un degre de detail spatial beaucoup plus important, disponible pour les pecheurs de germon sous la forme d'une souscription-abonnement auprès d'une compagnie (1) qui produit une valeur ajoutee au simple traitement d'images numeriques satellitaires. Des exemples de traitement graphique en degradé et de rehaussement par ligne de frontiere thermique et valeurs SST pour des zones tres representatives sont donnès dans la figure 9 (droit) et 9 (gauche) respectivement. Un traitement en fausses couleurs de l'imagerie thermique satellitaire est également disponible. Des cartes du même type que celles representees dans la figure 9 (droit), sont distribuees aux pêcheurs en mer par radio-fac-similé et les analyses en fausse couleur sont distribuées par poste express. Un nombre croissant de pêcheurs souscrivent ou s'abonnent a ce service en raison de la très fine resolution spatiale des frontières thermiques produites. Ceci aide réellement les pêcheurs à localiser les zones favorables a la pêche du germon.

Les structures thermiques proposées a partir de l'information satellitaire decrite ci-dessus sont generalement satisfaisantes pour repondre aux besoins de la pêcherie U.S. de germon lorsqu'ils pêchent a l'interieur d'une zone de 1 000 milles au large de la côte nord-américaine. Mais les zones au-dela de cette distance sont situees en dehors des zones de réception des stations de la côte ouest des U.S.A., pouvant recevoir des informations des satellites defilants a orbite polaire, qui passent au-dessus du Pacifique Nord. Il y a eu des tentatives de production de cartes d'isothermes et de frontieres thermiques à partir des mesures et enregistrements stockés à bord du satellite durant son passage au dehors des zones de réception des stations de la côte ouest des U.S.A.

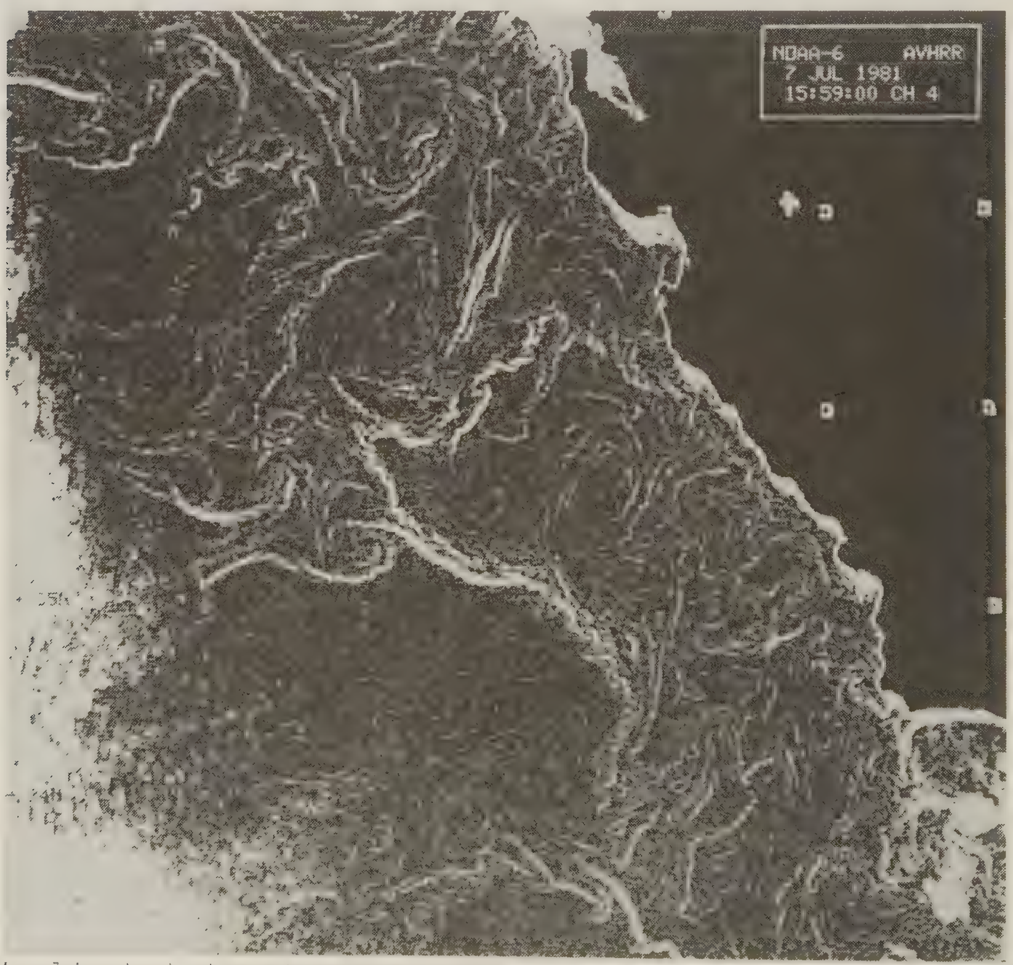
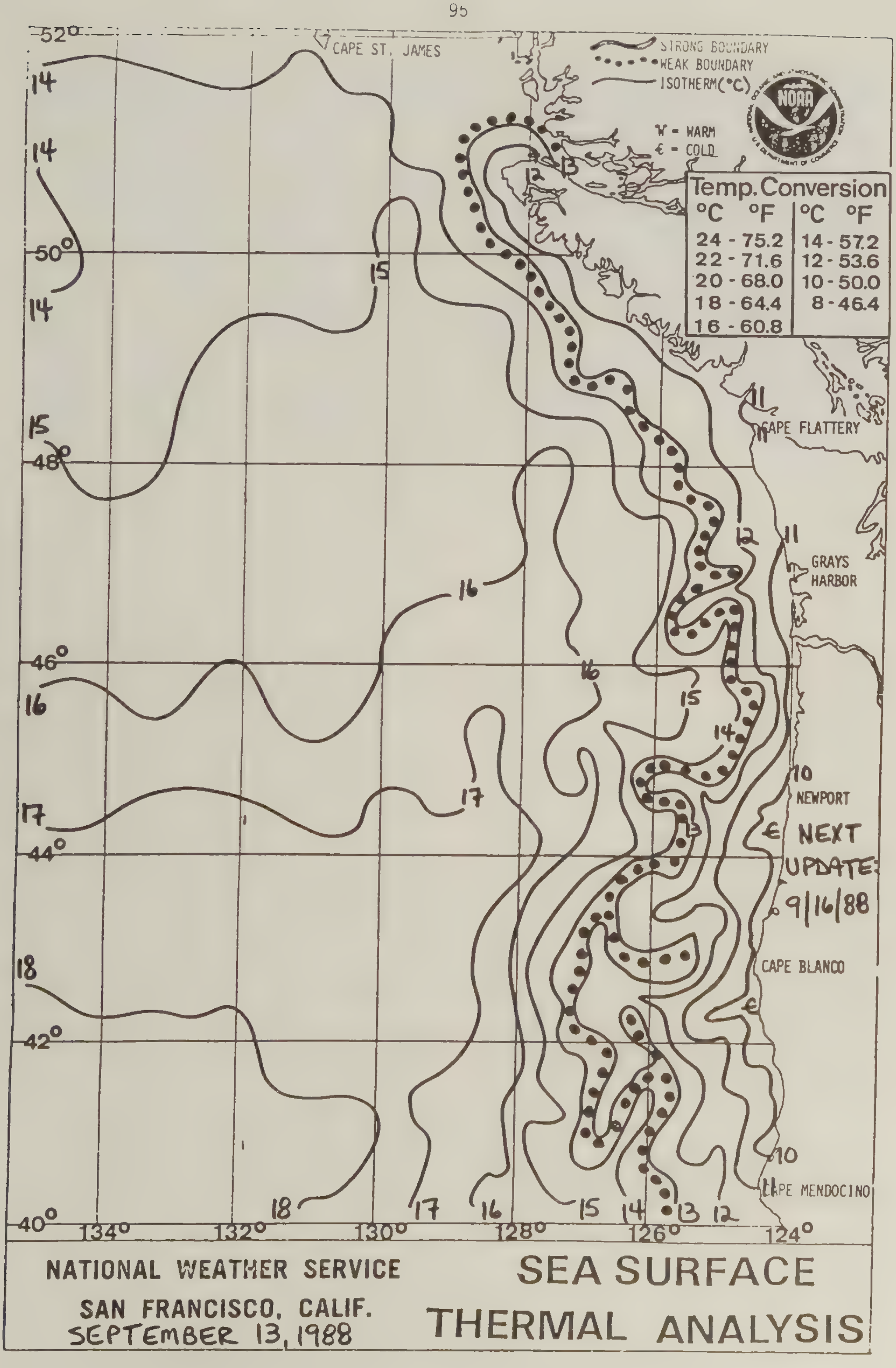


Figure 7 · Image de gradient thermique obtenu par filtrage AVHRR (adapte de Svegkovsky 1988)

---

(1) Ocean Imaging Company, San Diego, California, U.S.A; la réference à un nom de compagnie ou société n'engage pas la responsabilité de la NOAA/National Marine Fisheries Service.



Temp. Conversion

°C	°F	°C	°F
24	75.2	14	57.2
22	71.6	12	53.6
20	68.0	10	50.0
18	64.4	8	46.4
16	60.8		

Figure 8 - Exemple d'analyse de temperature de surface elabore a partir de l'imagerie satellitaire et de donnees de surface

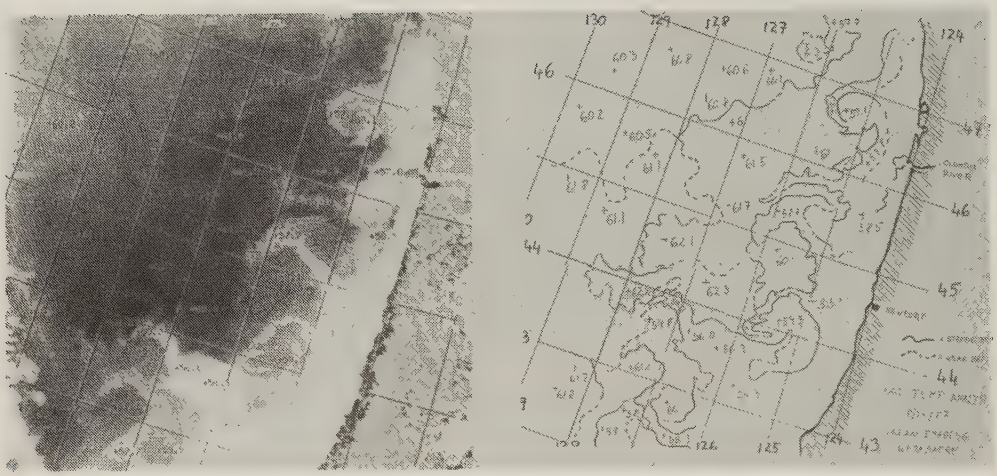


Figure 9. Deux analyses elaborees distribuees aux pecheurs par Ocean Imaging Company (gauche), image thermique en gris contraste avec une grille de positionnement et une surimposition de valeurs de temperature (droite) carte preparee pour la diffusion par radio-fac simile montrant l'analyse des frontieres thermiques et une surimposition des valeurs de temperature (aimablement fourni par Ocean Imaging Company, San Diego Californie)

Des essais ont ete tentes pour produire des cartes thermiques dérivees des donnees satellitaires au-dela de la zone des 1 000 miles au large de la côte ouest en utilisant ces donnees AVHRR obtenues par une station militaire de reception localisee a Hawaï. Ces essais n'ont pas été fructueux en raison du fort coût et des delais pour la livraison des enregistrements sur bande magnetique en Californie.

Afin d'obtenir une imagerie satellitaire lorsqu'ils operent dans des zones lointaines, quelques pêcheurs U.S. de germon ont achete, ou envisagent d'acheter, des equipements peu coûteux de reception et traitement definis pour la reception directe, traitement et visualisation a bord. Ces systemes recoivent une imagerie APT (Automatic Picture Transmission), dont les signaux dans le domaine du visible et de l'infrarouge thermique correspondent à des pixels de 4 km, a partir du systeme de satellite à orbite polaire. Ces systemes sont essentiellement diriges pour augmenter la securite en mer, et dans des zones sans couverture nuageuse fournissent une possibilite d'interpreter les champs thermiques superficiels pour une recherche plus efficace des zones de pêche.

Des systèmes de reception de donnees satellitaires APT embarques ont ete utilisees a bord de navires de recherche et de pêcheurs dans le Pacifique Central Sud durant la campagne exploratoire de pêche au germon (Laurs *et al.*, 1986 et Systems West, 1988). Les systèmes APT, constituent des equipements interessants et valable pour la realisation de frontieres thermiques associees a la zone de convergence sub-tropicale du Pacifique Sud ou de fortes captures de germon sont faites. En complement, les images de nuage demontrent l'utilite de systeme APT comme un outil pour accroitre la securite et l'efficacite des operations de pêche dans les zones caracterisees par une couverture meteorologique eparse et des previsions meteorologiques limitees.

De nombreux témoignages de satisfaction ont été reçus de la part des pêcheurs de germon américains et autres nationalites, à propos de l'utilite de l'information d'origine satellitaire pour l'aide a la localisation de zones favorables a la pêche. Selon les pêcheurs qui ont utilise largement des cartes « satellitaires », les analyses thermiques leur ont permis de gagner 25 à 30 % de leur temps de recherche et l'analyse des frontieres de couleur jusqu'à 50 % (Laurs, Communication personnelle fondee sur les interviews avec les pêcheurs). Cependant l'examen rigoureux de l'impact economique de l'utilisation de données satellitaires pour la pêche au germon n'a pas ete réalise.

Remerciement

Une partie du travail évoque dans cette revue a bénéficié d'un financement de la National Aéronautics ans Space Administration, Orders W-15,334 and W-16,509.

Références

Breaker, L.C. and F. Jurick, 1975. Providing near real-time sea surface temperatures to the California north coast fishing fleet : an approach. In : *Ocean 75* (Combined meeting of 1975 IEEE Conference on Engineering in the Ocean Environment and 11th Annual Meeting of the Marine Technology Society), San Diego, California, New York Institute of Electrical and Electronic Engineers, Inc. 952 pp.

Breaker, L.C., 1981. The application of satellite remote sensing to West Coast fisheries. J. Mar. Tech. Soc. 15 : 32-40.

Clark, D.K., 1981. Phytoplankton pigments algorithms form the Nimbus-7 CZCS. In : *Oceanography form space*, edited by J.F.R. Gower. Plenum Press. New York pp. 227-238.

Fiedler, P.C., G.B. Smith, R.M. Laurs, 1985. Fisheries applications of satellite data in the North Pacific. Mar. Fish. Rev. 46 : 1-13.

Jurick, F.A., 1985. A comparison between North Pacific commercial albacore (*Thunnus alalunga)* catch and the satellite derived West Coast thermal boundary analysis. M.S. Thesis, Humbolt State University, Arcata, California, 79 pp.

Lauritson, L., G.G. Nelson and R.W. Porto, 1979. Data extraction and calibration of TIROS-N/NOAA radiometers. NOAA, Tech. Memo. NESS 197 : 44-46.

Laurs, R.M., 1971. Fishery-Advisory information available to tropical pacific tuna fleet via radio facsimile broadcast. Comm. Fish. Rev. 33 : 40-42.

Laurs, R.M., C. Hooker, L. Hreha and R. Lincoln, 1975. A uniform U.S. West Coast log book for albacore, *Thunnus alalunga* (Bonnaterre), and coastwide albacore fishery data system. Mar. Fish. Rev. 37 : 14-21.

Laurs, R.M., Clemens and L.H. Hreha, 1976. Nominal catch-per-unit effort of albacore, *Thunnus alalunga* (Bonnaterre), caught by U.S. jig vessels during 1961-1970. Mar. Fish Rev. 38 : 1-32.

Laurs, R.M., 1977. Albacore advisory fish bulletins : 77-3 through 77-9. National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California. 7 pp

Laurs, R.M., and R.J. Lynn, 1977. Seasonal migration of North Pacific albacore, (*Thunnus alalunga)*, into North American coastal waters : distribution, relative abundance, and association with Transition Zone waters. Fish. Bull. NOAA, U.S. Dept. of Commerce, 75 : 795-822.

Laurs, R.M., H.S.H. Yuen and J.H. Johnson, 1977. Small-scale movements of albacore (*Thunnus alalunga)*, in relation to Ocean features as indicated by ultrasonic tracking and oceanographic sampling. Fish. Bull. NOAA, U.S. Dept. of Commerce, 75 : 347-355

Laurs, R.M., R.J. Lynn, R. Nishimoto and R. Dotson, 1981. Albacore trolling and longline exploration in eastern North Pacific waters during mid-winter 1981. NOAA Technical Memorandum NMFS 10. 52 pp.

Laurs, R.M., R.C. Dotson, A. Dizon and A. Jamison, 1980. Observations on swimming depth and ocean temperature telemetered from free-swimming albacore. In : *Proceeding of 31st Tuna Conference* (May 11-14, 1980), edited by A Wild, La Jolla : Inter-American Tropical Tuna Commission. pp. 33-34.

Laurs, R.M., P.C. Fiedler, and D.R. Montgomery, 1984. Albacore tuna catch distributions relative to environmental features observed from satellites. Deep Sea Res. 31 : 1085-1099

Laurs, R.M. and J T. Brucks, 1985. Living Marine Resources Applications. In : *Advances in Geophysics, Satellite Oceanic Remote Sensing*, edited by Barry Saltzmen. Academic Press, London, Vol. 27, pp. 419-450.

Laurs, R.M., K.A. Bliss and J.A. Wetherall, 1986. Preliminary Results from R/V *Townsend Cromwell* South Pacific Research Survey. NOAA, Nat. Mar. Fish. Serv., Southwest Fisheries Center, Admin. Rep. LJ-86-13. 80 pp.

Laurs, R.M., J. Svejkovsky and M.W. Hess, (in prep.) A case study relating variations in albacore tuna fishing success and habitat to oceanographic and marine weather conditions measured by satellite scatterometer, altimeter and infrared sensor.

McClain E.P., W.E. Pichel, C.C. Walton, Z. Ahmadd and J. Sutton, 1983. Multichannel improvements to satellite-derived global sea surface temperatures. Advances in Space Res. 2 : 43-47.

Miyabe, N. and N. Bartoo, 1987. Report of the tenth North Pacific albacore workshop. NOAA, Nat. Mar. Fish. Serv., Admin. Rep. LJ-87-27, La Jolla, California, 19 pp.

Montgomery, D.R., R.E. Wittenberg-Fay and R.W. Austin, 1986. The applications of satellite-derived ocean color products to commercial fishing operations. Mar. Technol. Soc. J. 20 : 72-86.

Njoku, E.G., 1985. Satellite-derived sea surface temperature : Workshop comparisons. Bull. Amer. Meteorol. Soc. 66 : 274-281.

Pearcy, W.G. and J.L. Mueller, 1970. Upwelling, Columbia River plume and albacore tuna. Proc. of the 6th Int. Symp. on Remote Sensing of the Environment, Univ. of Mich., pp. 1101-1113.

Short, K., 1979. How Satellites can help you catch more fish and cut costs. Nat. Fish. 60 : 38-39.

Smith, R.C. and W.H. Wilson, 1981. Ship and satellite bio-optical research in the California Bight. In : *Oceanography from Space*, J.F.R. Gower, editor, Plenum Press, New York, pp. 281-294.

Svejkovsky, J., 1988. Remotely sensed ocean features and their relation to fish distributions. In : *Marine Organisms as Indicators*, edited by D.F. Soule and G.S. Klepple, Springer-Verlag, New York, pp. 177-197.

System West Inc., 1988. Final report for work performed under the Saltonstall-Kennedy Grant no. NA-88-ABH-00021, submitted to National Marine Fisheries Service, Regional Office, Terminal Island, California. 33 pp.

Uda, M., 1973. Pulsative fluctuation of oceanic fronts in association with tuna fishing grounds and fisheries. J. Fac Mar. Sci. Technol., Tokai Univ. 7 : 245-265

8935

REVIEW OF SATELLITE APPLICATIONS TO FISHERIES

R. Michael Laurs

National Oceanic & Atmospheric Administration
National Marine Fisheries Service
P.O. Box 271
La Jolla, CA 92038 USA

ABSTRACT

Satellite oceanic remote sensing applications to fisheries research and fish harvesting in the U.S. are reviewed. Specific case studies are discussed to show how satellite data have been used in fisheries that are marketed as different types of fishery products. These include albacore tuna which is marketed primarily as a canned product, northern anchovy which are reduced for meal and industrial products, Pacific salmon species marketed mostly as fresh and fresh-frozen table fish, and Gulf of Mexico shrimp which are marketed mostly fresh.

INTRODUCTION

Satellite oceanic remote sensing can be a very powerful tool when used in fisheries research and in harvesting marine resources. The successes gained in experiences using satellite data in fisheries investigations and in harvesting thus far, indicate there is immense potential for expanding its utilization. Satellite remote sensing can supply environmental information, which can lead to improvements needed to ensure the effective management of marine fishery resources. It also, can provide information to detect potentially productive fishing grounds and to make improved weather and sea condition forecasts for the safety of fishermen and their vessels and equipment.

Variations in ocean conditions play crucial roles in causing natural fluctuations of fisheries resources and their vulnerability to catch. Comprehensive information on the changing ocean, rather than on average ocean conditions, is needed to effectively manage many stocks of living marine resources and to efficiently harvest them.

The strength of satellite remote sensing lies in the ability of spacecraft sensors to monitor ocean variability with the combined advantages of large scale synopticity, high spatial resolution and frequent repeatability. Each of these characteristics is prerequisite to understanding the effects of ocean variability on fishery resources.

Despite its strengths, satellite remote sensing has weaknesses, chief of which is the capability of sensors to measure only the surface skin or uppermost layer of the ocean. In addition, most present sensors provide useful data only in cloud- free areas. The application of satellite remote sensing to fisheries has also been hampered by difficulties in obtaining satellite data, the lack of affordable systems to process it, and by a shortage of trained people needed to conduct research and development and education of fisheries users. However, recent advances in the capabilities of data-processing systems and improved training opportunities in satellite oceanography, offer promise for the future.

In this manuscript, after a brief over-view of satellite data used in fisheries, experiences are summarized from marine fisheries investigations which have utilized satellite data. Specific examples have been selected to show how satellite data have been used in fisheries that are marketed as different types of fishery products including: albacore tuna which are marketed primarily canned, chinook and coho salmon which are sold fresh, northern anchovy which are reduced for meal and industrial products, and Gulf of Mexico shrimp which have several types of markets.

SATELLITE DATA USED IN FISHERIES

Satellite measurements that have been used in fisheries applications are: ocean temperature and color and ocean wind stress. Most fisheries research studies and operational uses of satellite sea surface temperature (SST) measurements have utilized data from thermal infrared sensors onboard the TIROS polar-orbiting meteorological satellites. Some have also used infrared data from geostationary satellites. However, only a very limited number of attempts have been made to apply ocean temperature measurements made by microwave instruments. The Coastal Zone Color Scanner (CZCS) on the Nimbus-7 satellite provided color measurements from space from early 1979 to about mid-1985. The excellent ocean color data from the CZCS have probably been more valuable for fisheries uses than any other ocean measurements made from space. There has been very limited success in using Landsat color imagery in fisheries studies. The scatterometer (SASS) aboard the Seasat-A satellite furnished data which demonstrated the importance to fisheries of high resolution surface wind stress measurements from space. Satellite wind stress measurements can be used to calculate ocean surface layer transport, which controls the distribution of larval stages and the subsequent recruitment and harvests of many marine fishes and shrimps. Satellite measurements of ocean winds can also be extremely valuable in the detection and forecast of weather and sea conditions hazardous to safety at sea.

EXAMPLES OF SATELLITE APPLICATIONS TO FISHERIES

Albacore Tuna - A Canned Product Fishery

Albacore are highly mobile tuna which are widely distributed throughout the world's oceans. In the North Pacific Ocean, they migrate seasonally into waters off the coast of North America during July through October, where they support important U.S. commercial and recreational fisheries. Most of the albacore caught by commercial fisheries is consumed as a canned product. The distribution, availability and vulnerability of albacore off the west coast of the U.S. have been found to be related to oceanic fronts seen in AVHRR infrared and CZCS imagery (Laurs et al., 1984; Jurick, 1985; and Svejkovsky, 1987).

An investigation employing AVHRR infrared temperature and CZCS color imagery and concurrent daily commercial fishing catch records clearly showed that satellite temperature and color data can be used to define the environmental limits of the spatial distribution of fishable aggregations of albacore, and can do so more effectively than ship or aircraft data (Laurs et al., 1984). This study convincingly demonstrated that the distribution and availability of albacore off the west coast of California are related to oceanic fronts associated with coastal upwelling. Commercially fishable aggregations of albacore are found in warm, blue oceanic waters near temperature and color fronts that mark the seaward edge of waters which had been upwelled near the coast. Relatively intense fronts are favored and shoreward intrusions of warm, clear oceanic water are particularly favorable sites for albacore concentration. This study also found that during late summer, commercial concentrations of albacore several hundreds of miles offshore, were associated with oceanic boundaries noted by color fronts detectable from satellite, but without temperature gradients. The color boundaries probably distinguished the North Pacific Subtropical Front. In another study, the distribution of albacore in winter was linked to SST fronts observed in AVHRR imagery, which probably to mark the outer boundary of the California Current. (Laurs et al., 1981).

Possible mechanisms responsible for the aggregations of albacore in the vicinity of upwelling boundaries is being investigated using data from acoustic tracking of free-swimming albacore and concurrently collected oceanographic data from ships and AVHRR and CZCS data from satellites. The results suggest that albacore aggregate on the warm, clear oceanic side of coastal upwelling boundaries and avoid areas of higher productivity and forage density in upwelled waters, because they are not able to detect prey in the turbid, upwelled water. (Laurs, in prep.).

U.S. albacore fishermen make extensive use of satellite-derived fishery advisory products for determining favorable locations to fish and for safety. SST analyses based on satellite data have been routinely available for nearshore coastal waters off the U.S. west coast since 1975 (Breaker and Jurick, 1975). The format, degree of detail, and methods of dissemination of these analyses, which are in chart form, have varied over the years (Breaker, 1981). Presently, they consist of large-scale thermal boundaries which are derived from AVHRR imagery, and isotherms which are based mostly on in situ observations from ships and buoys. The charts are prepared twice a week and are distributed to fishermen by radio facsimile and by mail.

An AVHRR infrared sea surface temperature analysis for west coast waters, with considerable more detail is available to fishermen on a subscription basis from Ocean Imaging Company in San Diego, California. The satellite derived thermal analysis charts are distributed to fishermen at sea by radio facsimile, or photographs with false-color are disseminated by express mail or hand delivery. An increasing number of albacore and other fishermen subscribe to these ocean products because they are specially tailored to meet their needs, including high spatial resolution of surface boundary features.

To obtain satellite imagery when operating in distant water locations, some albacore fishermen have purchased low-cost systems designed for direct reception, processing and display of satellite imagery on board ship. These systems receive visual and infrared imagery with a 4 km pixel size by Automatic Picture Transmission (APT) signals directly from polar-orbiting satellites. The visual imagery is used to help avoid areas of hazardous weather, and the infrared imagery is being used to interpret SST patterns for more efficient track and fishing ground selection, in cloud-free areas.

During the early 1980's and continuing until the CZCS sensor failed, ocean color boundary charts based on CZCS imagery were utilized by U.S. west coast albacore to locate potentially favorable locations to fish (Montgomery et al., 1986). These charts were prepared and disseminated via radio facsimile in a program funded by the Jet Propulsion Laboratory and involving Scripps Institution of Oceanography and the U.S. National Marine Fisheries Service. According to surveys of fishermen, these satellite-derived ocean products were remarkably useful in locating favorable areas to fish for albacore, and could save them as much as 50% in search time.

Oregon Coho and Chinook Salmons - A Fresh Market Fishery

Chinook and coho salmon support lucrative markets as fresh fish products. An investigation is underway to evaluate the use of satellite imagery to determine the optimal time of release of salmon smolts from hatcheries on the Columbia River to correspond with ocean conditions favorable for their survival. Increasing the survival and subsequent contribution of salmon released from hatcheries to commercial and recreational fisheries can have significant economic benefit.

Up to 90% of the salmon caught in the waters off the Columbia River are released from hatcheries on the Columbia River. About 60% of the salmon caught in other areas off the Pacific Northwest are from salmon released from hatcheries on other coastal rivers and streams. While hatchery produced salmon contribute most of the fish which are harvested, the percentage of fish released that are caught is low, e.g. only about 2% for Columbia River hatcheries. About 98% of the salmon that are released suffer mortality. A major part of the mortality is believed to occur in the ocean soon after the smolts arrive there, subsequent to their release from the hatcheries (Pearcy, 1984).

The research is directed toward testing the hypothesis that the survival of young salmon released from Columbia River hatcheries is related to variations in characteristics of the Columbia River plume and its interactions with other oceanic processes, notably coastal upwelling. The goal of the research is to ascertain if satellite imagery can be used to determine when ocean conditions are favorable for young salmon, so that the release of the smolts from hatcheries may be timed for optimal survival. Even modest increases in survival could result in substantial increases in salmon available for harvest, and have significant economic value.

Findings thus far have demonstrated that ocean temperature and phytoplankton pigment images derived from AVHRR and CZCS data, respectively, show that the Columbia River plume has remarkable variability in coastal waters off the Pacific Northwest (Fiedler and Laurs, in review). The orientation, shape, intensity and relative temperature of the plume vary in response to coastal winds and wind-driven surface currents.

The use of satellite-derived SST distribution and frontal boundary analyses by commercial fishermen to locate potentially fruitful locations to catch fish is a further application of satellite remote sensing to Pacific Northwest salmon resources.

Northern Anchovy - A Fishery Where Catches are Reduced For Oil and Industrial Uses

Northern anchovy, *Engraulis mordax*, is a California Current fish targeted for an oil and meal reduction fishery. Like most fish species harvested for their oil and meal, the anchovy is relatively short-lived and spends its early life history stages, part of which are planktonic, in the upper mixed layer. Its spawning, early survival and recruitment to the fishery are believed to be largely controlled by ocean conditions (Lasker, 1978).

Satellite imagery has been used to investigate ocean processes in relation to northern anchovy spawning. In these studies, which were conducted for several years during anchovy spawning periods, satellite data were collected on a daily basis coincident with fine-grid oceanographic ship observations. Shipboard observations included sampling of anchovy eggs, larvae and adults as well as physical oceanographic measurements. The objectives of the investigations were to relate variations in mesoscale SST distributions (Lasker et al., 1981) and phytoplankton pigment and SST distributions (Fiedler, 1983) with anchovy spawning, and to identify and delineate ocean processes that might be important to the survival of fish eggs and larvae. Based on satellite imagery and confirmed by shipboard observations during the studies, which were conducted in the Southern California Bight, there were were distinct temperature and pigment regimes in the general geographic region where anchovy spawning normally takes place.

Lasker et al. (1981) found that anchovy avoid recently upwelled water and that the areal extent of upwelled water may be mapped using infrared satellite imagery. They concluded that the anchovy habitat for spawning in the northern part of the Southern California Bight could be defined using AVHRR satellite data. Fiedler (1983) corroborated Lasker et al. (1981) conclusion and also found that the limits of the spawning habitat in the southern part of the Bight could be differentiated using CZCS imagery. The spatial distribution of northern anchovy spawning can thus be defined by mesoscale patterns in satellite temperature and phytoplankton pigment images (Lasker et al, 1981 and Fiedler, 1983). While neither parameter alone is sufficient, both together may define the spatial distributions nearly completely. In general, the northern extent of spawning in the Southern California Bight and the offshore extent north of Santa Catalina Island are limited by cold, upwelled water advected south of Point Conception. Spawning to the south is limited by low phytoplankton pigment levels in oceanic water 20-100 km offshore rather than by temperature. However, these factors do not directly determine spawning success, but rather are indicators of oceanic conditions and processes that determine the spawning habitat.

Fiedler (1984) also demonstrated the effectiveness of using satellite AVHRR and CZCS imagery to monitor shifts in anchovy spawning habitat off California associated with the 1982-1983 El Niño warm-water conditions.

Shrimp In The Gulf Of Mexico - Mostly a Fresh Product Fishery

Surface layer transport processes play an critical role in the life cycle of shrimp. Dispersal mechanisms control the distribution of early life stages of shrimp and the transport of developmental stages from offshore waters to coastal estuarine areas in the Gulf of Mexico. Thus the recruitment and future harvest of shrimp resources are determined, in large, part by ocean surface layer transport.

Brucks et al., in prep., also see Laurs and Brucks (1985), conducted a case study to investigate whether high-resolution measurements of wind stress by the Seasat-A scatterometer (SASS) could improve estimates of surface layer and larval shrimp transport based on traditional geophysical models. The SASS- measured wind-stress field was used to calculate surface currents by the standard homogeneous, steady-state Ekman solution. The SASS approach reduces the number of assumptions involved in the calculation of the wind-stress vector and presumably provides more accurate estimates of surface circulation. Striking spatial and temporal variability in wind-drift pattern and regions of convergence and divergence were apparent in the Gulf of Mexico using the SASS wind-stress data to calculate surface-layer transport processes. The investigators used surface-layer transport estimates calculated from the SASS data to define potential offshore areas where shrimp spawn material and very early-life stages could be rich in the plankton and coastal areas where larval and post-larval planktonic stages could accumulate prior to settling. They found that processes conducive for accumulation in the offshore regime mainly in the west central Gulf and some projections to the south, west and north. The predicted coastal areas were in close proximity to shrimp nursery grounds in Louisiana, Texas and Florida.

Brucks et al. concluded that synoptic and repetitive direct measurements of wind stress by the SASS provided a significantly enhanced capability to determine variability in wind-driven events that strongly influence shrimp recruitment processes in the Gulf of Mexico.

LITERATURE CITED

1. Brucks, J.T., T.D. Leming, and S.B. Buokett, Jr., "A model investigation using high resolution SASS wind stress measurements to derive wind surface layer transport properties in the Gulf of Mexico", In prep.

2. Breaker, L.C., "The application of satellite remote sensing to west coast fisheries", J. Mar. Tech. Soc. Vol.15, pp32-49, 1981.

3. Breaker, L.C. and F.A. Jurick., "Providing near real-time sea surface temperatures to the California north coast fishing fleet", In: Ocean 75 (Combined meeting of 1975 IEEE Conference on Engineering in the Ocean Environment and 11th Annual Meeting of the Marine Technology Society), San Diego, Calif., N.Y. IEEE, 952pp, 1975.

4. Fiedler, P.C., "Satellite remote sensing of the habitat of spawning anchovy in the Southern California Bight", CalCOFI Rep. No. 24, pp202-209, 1983.

5. Fiedler, P.C., "Some effects of El Niño 1983 on the northern anchovy", CalCOFI Rep. No.25, pp53-58, 1984.

6. Fiedler, P.C. and R.M. Laurs, "Variability of the Columbia River plume observed in visible and infrared satellite imagery", Remote Sensing Environ., In rev.

7. Jurick, F.A., "A comparison between North Pacific commercial albacore *(Thunnus alalunga)* catch and the satellite derived West Coast thermal boundary analysis", M.S. Thesis, Humboldt State University, Arcata, Calif., 79pp, 1985.

8. Lasker, R., "The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure",Rapp. P.-V. des Reun. Cons. int. Explor. Mer. Vol.173, pp212-230, 1978.

9. Lasker, R., J. Pelaez and R.M. Laurs, "The use of satellite infrared imagery for describing ocean processes in relation to spawning of northern anchovy *(Engraulis mordax)*", Remote Sensing Environ., Vol.11, pp439-453, 1981.

10. Laurs, R.M., "The role of water clarity in albacore aggregations in upwelling frontal areas", In prep.

11. Laurs, R.M. and J. Brucks, "Living marine resouces applications", In Satellite Oceanic Remote Sensing, Ed. B. Saltzman, Adv. Geophys., Vol.27, pp419-452, 1985.

12. Laurs, R.M., R.J. Lynn, R. Nishimoto, and R. Dotson, "Albacore trolling and longline exploration in eastern North Pacific water during mid-winter 1981", NOAA Tech. Memor., NMFS-SWFC-10, 52pp, 1981.

13. Laurs, R.M., P.C. Fiedler, and D. Montgomery,"Albacore tuna catch distributions relative to environmental features observed from satellites", Deep Sea Res., Vol.31, pp1085-1099, 1984.

14. Montgomery, D.R., R.E. Wittenberg-Fay, and R.W. Austin, "The applications of satellite-derived ocean color products to commercial fishing operations", MTS Jour. Vol.20, No.2, 72-86, 1986.

15. Pearcy, W.G., "The influence of ocean conditions on the production of salmonids in the North Pacific, a workshop", Oregon State Univ., Sea Grant College Program, ORESU-W-83-001, Corvallis, Oregon, 327pp, 1984.

16. Svejkovsky, J., "Remotely Sensed Ocean Features and Their Relation to Fish Distributions", In: Organisms As Indicators, Eds. G. Kleppel and D.F. Soule, Springer-Verlag Publishers, N.Y., pp179-197, 1987.

8936

SPERM CONCENTRATIONS AND EGG FERTILIZATION RATES DURING SPAWNING OF CAPTIVE ANCHOVY, *ENGRAULIS MORDAX*

RODERICK J. H. LEONG
National Marine Fisheries Service
Southwest Fisheries Center
P.O. Box 271
La Jolla, California 92038

ABSTRACT

The minimum sperm density needed for maximal fertilization success was determined for northern anchovy. On the average, 90% of anchovy eggs were fertilized in a concentration of 100 or more sperm per ml. These results were obtained by varying the number of hormone-treated male and female northern anchovy spawned in 3-m^3 tanks and examining the egg fertilization rate. These results were compared with two other studies.

RESUMEN

Se determinó la densidad mínima de esperma necesaria para maximizar el éxito de fecundación de la anchoa del Pacífico norte. En promedio, 90% de los huevos de anchoa fueron fertilizados con una concentración de 100 ó más espermas por mililitro. Estos resultados fueron obtenidos variando el número de machos y hembras de anchoa, desovados en tanques de $3\ \text{m}^3$ y previamente tratados con hormonas, y examinando posteriormente la tasa de fecundación de los huevos. Estos resultados fueron comparados con dos estudios previos.

INTRODUCTION

Only a small percentage of the anchovy eggs collected during the CalCOFI cruises have been identified as being undeveloped. Thus the northern anchovy may have evolved a mode of spawning in which nearly every egg contacts sperm in sufficient numbers for fertilization. The concentrations of sperm required for high rates of fertilization, and the role of the male in establishing these concentrations have been observed in only a few fishes and never in pelagic spawners. This report presents laboratory observations on the concentration of sperm in the water at the time of anchovy spawning, and on how that concentration relates to the fertilization rate.

MATERIALS AND METHODS

The concentration of sperm in the spawning tank, and the percentage of eggs fertilized were estimated for 19 spawning trials. Each trial consisted of a hormone-induced spawning and the collection of sperm and egg samples immediately after detection of eggs in the water. Collected anchovy were acclimated to the holding tanks for several months before hormone treatments, and the trials began only when the majority of fish had well-developed gonads.

The fish were induced to spawn with a procedure modified from Leong 1971; the females received 50 I.U. of human chorionic gonadotropin and 5 mg of carp pituitary, while the males received only 50 I.U. of human chorionic gonadotropin. The injection on the first day, 50 I.U. of human chorionic gonadotropin, was given to all fish. On the following day, all fish were squeezed, and males were identified by the secretion of milt. Fish that did not secrete milt when squeezed were assumed to be females and given the second injection. The number of males was reduced in some trials to lower sperm density.

Shedding of eggs began spontaneously 35 to 42 hours after the first injection. A strainer was passed through the water at half-hour intervals to determine when eggs were released. The spawning tank was slightly more than 3 m in diameter and contained $2.96\ \text{m}^3$ of water with a depth of .41 m. The flow-through tank had a water flow rate of 15 liters per minute, and the spawning temperature was about 17°C. The salinity averaged 32‰.

Three water samples provided an estimate of the average sperm concentration in the spawning tank during a trial. The samples, 100 ml in volume, were taken at mid-depth from different areas of the pool. Two drops of rose bengal stain and two ml of concentrated Formalin were added to each sample to stain and preserve the spermatozoa. Immediately after collection, each sample was passed through a millipore filter (0.25-µm pore size and 25-mm diameter) under slight vacuum to separate and concentrate the spermatozoa, which have a head 4 µm × 1.3 µm and a tail about 55 µm long (figure 1). The filter was placed on a microscope slide with immersion oil and warmed to clarify the filter and make the spermatozoa visible.[1] I estimated the

---

[Manuscript received February 2, 1989.]

[1] A brochure by the Millipore Corporation gives further details on the clarification and use of millipore filters.

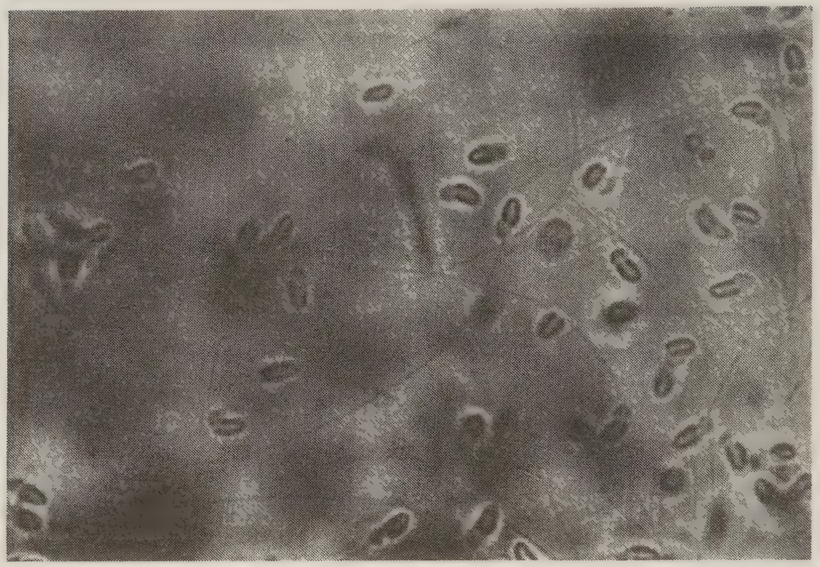


Figure 1. Anchovy sperm (photo by Bev Macewicz). Head 4 µm × 1.3 µm; tail ~ 55µm.

number of spermatozoa on the filter by counting the number in several transects of measured lengths and widths with an inverted microscope at 400X magnification. I counted at least 300 sperm per filter except at the lowest concentration. Estimates made by the millipore filter method were compared to estimates made with a hemacytometer for five milt samples to test the technique (table 1). The milt were diluted 1:20,000 for counting with the hemacytometer and 1:20,000,000 for the millipore filter. The sperm densities estimated by the two methods did not differ statistically ($t = 4.54$; $p < .05$).

All fish in a trial were used only once and were killed at the end of the trial. Routine measurements on males included length, weight, testes weight, and gonadosomatic index (percentage testes weight of body weight).

The egg fertilization rate was determined by examining 200–300 eggs for signs of development. The eggs were collected soon after the detection of spawning and incubated in a beaker for an hour before examination. Developing eggs were easy to distinguish during the early stages of cell division, with pictures from Moser and Ahlstrom (1985) and Bolin (1936) as guides. Eggs that did not develop after the one-hour waiting period were assumed to be unfertilized.

RESULTS AND DISCUSSION

The estimated density of sperm in the water of the spawning tank, percentage of eggs fertilized, and other pertinent data from each of the 19 trials are given in table 2. The relation between the egg fertilization rate and density of sperm appears in figure 2. The figure shows the fertilization rate increasing with higher sperm density for densities up to 100 ml^{-1}; maximum rates begin to appear near that level. The regression equation for observations with less than 100 sperm ml^{-1}, $Y = 1.00$, indicates that the rise in egg fertilization was proportional to the density of sperm for the trials, and indicates a 50% level of fertilization for a sperm density of 50 ml^{-1}. The regression equation for observations with sperm density greater than 100 ml^{-1}, $Y = 88.1 + 0.0007$, suggests a slight increase in fertilization rate with higher sperm density, but the slope was not significantly different from zero. The average fertilization rate for sperm densities above 100 ml^{-1} was 88.9%, with a range of 70.1% to 99.0%. Some of the lower rates were probably due to imperfec-

TABLE 1
Comparison of Two Methods Used to Count Sperm

Milt sample	Hemacytometer estimate (10^9)	Millipore filter estimate (10^9)	Ratio of millipore to hemacytometer estimate
1	6.76	4.00	.59
2	6.28	5.92	.94
3	7.88	6.74	.86
4	8.04	8.78	1.09
5	8.64	9.66	1.12
$\bar{x}$	7.52	7.02	.92

TABLE 2
Estimated Density of Sperm and Percentage of Eggs Fertilized When Anchovy Were Induced to Spawn in the Laboratory

Trial	Estimated sperm density in water of spawning tank (n/ml^{-1})[a]	Percentage of eggs fertilized	Number of fish		Average male gonosomatic index (%)[c]
			Male[b]	Female	
1	9013	93.0	17	19	7.8
2	1435	98.0	4	19	6.4
3	862	98.0	18	—	4.7
4	744	80.1	14	11	6.1
5	337	99.0	14	18	10.9
6	268	90.0	25	35	8.7
7	217	70.1	6	20	10.1
8	165	80.0	1	16	8.6
9	141	84.6	17	14	7.3
10	122	96.4	18	17	8.3
11	97	97.0	19	16	3.7
12	87	84.0	11	22	6.9
13	86	89.2	27	14	7.9
14	78	70.0	8	10	8.0
15	66	60.2	13	—	9.4
16	55	80.0	8	16	8.3
17	50	54.2	2	14	4.8
18	25	18.5	11	16	5.1
19	4	4.4	2	15	13.0

[a] Estimated from three 100-ml water samples from spawning tank containing 2.96 m^3 water.
[b] Average male length was 116.6 mm; average weight was 21.0 g.
[c] Postspawning testes weight ÷ body weight × 100.

tions in the induced spawning procedure, which in some cases may have stimulated the release of immature gametes.

The rough relationships between sperm density and the number of males suggest that the number of sperm released per male was highly variable. The average concentration of sperm in the water may not be the same as the concentration surrounding newly extruded ova. In many species the male deposits sperm directly over the newly spawned eggs (Breder and Rosen 1966), and in those situations the eggs are surrounded by sperm at a much higher concentration than that surrounding the average egg in the water column. However, I did not see any close interaction between the sexes during the trials. Members in the spawning school usually milled about slowly and did not display any obvious behavior patterns such as pairing or posturing to indicate that spawning was in progress; yet my samples indicated that spawning had occurred. The sexes may have simply released gametes into the water, perhaps with some synchrony but without apparent change in behavior. If the spawning anchovy simply released gametes into the water without pairing and body contact, then the eggs were fertilized in water containing the observed sperm concentrations. Whether the simple mode of spawning I observed in the laboratory also occurs in the sea is unknown. Anchovy spawn only at night (Smith and Hewitt 1985; Bolin 1936), and the dark conditions could possibly limit the use of visual cues in their spawning behavior.

The minimum sperm density needed for maximal fertilization success has been studied in only a few teleosts, and the results have been varied. Ginzburg (1972) studied the problem by placing roe with

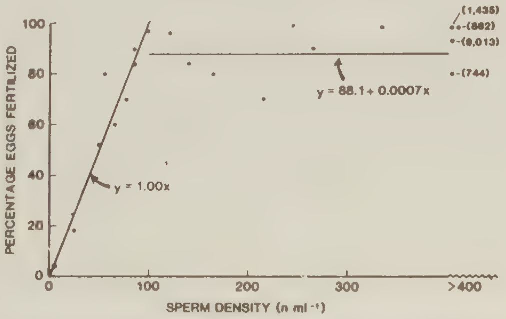


Figure 2. Percentage of eggs fertilized and sperm density during induced spawning of northern anchovy. Density is number of sperm ml^{-1} water of spawning tank. Densities greater than 400 ml^{-1} are in parenthesis.

stripped milt in various dilutions and found that concentrations of 10^{5}–10^{6} sperm ml^{-1} were necessary for maximum fertilization in certain salmonids and sturgeon. In a different setting Hourston and Rosenthal (1976) sampled surface water of milky discoloration above a school of spawning herring *Clupea harengus palasii* and found concentrations of 148 and 129 sperm ml^{-1}, which they theorized to be more than ample for high fertilization success.[2] The sperm densities at which maximum fertilization occurred in the present study are close to those observed by Hourston and Rosenthal, but magnitudes lower than those observed by Ginzburg. Additional studies would be required to resolve these differences.

In any future work, other factors such as swimming speed and longevity, length of time ova are receptive to sperm, properties in the egg that may attract or activate sperm, and temperature should be considered as well as sperm density; only sperm density was considered in this study.

ACKNOWLEDGMENTS

I thank John Hunter, Paul Smith, and Gail Theilacker for reviewing the manuscript and making useful suggestions, and Eric Lynn for his help during the trials.

LITERATURE CITED

Bolin, R. L. 1936. Embryonic and early larval stages of the California anchovy, *Engraulis mordax* Girard. Calif. Fish Game 22(4):314–321.

Breder, C. M., Jr., and D. E. Rosen. 1966. Modes of reproduction in fishes. New York: Natural History Press, 941 pp.

Ginzburg, A. S. 1972. Fertilization in fishes and the problem of polyspermy. Jerusalem: Keter Press. Translated from Russian. Available from U.S. Department of Commerce, NTIS, Springfield, Virginia, 366 pp.

Hourston, A. S., and H. Rosenthal. 1976. Sperm density during active spawning of Pacific herring (*Clupea harengus pallasi*). J. Fish. Res. Board Can. 33:1788–1790.

Leong, R. 1971. Induced spawning of the northern anchovy, *Engraulis mordax* Girard. Fish. Bull., U.S. 69(2):357–360.

Moser, H. G., and E. H. Ahlstrom. 1985. Staging anchovy eggs. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, R. Lasker, ed. U.S. Dep. Commer., NOAA Tech. Rep. NMFS-36, pp. 37–41.

Smith, P. E., and R. P. Hewitt. 1985. Sea survey design and analysis for an egg production method of anchovy biomass assessment. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, R. Lasker, ed. U.S. Dep. Commer., NOAA Tech. Rep. NMFS-36, pp. 17–26.

---

[2] Hourston and Rosenthal calculated that a herring egg would attract 24 sperm when the density is 150 ml^{-1}, but P. E. Smith, NMFS, La Jolla, personal communication, found an error in their calculation; the number attracted should be corrected to 0.024.

8937

S. Afr. J. mar. Sci. 8: 195-205
1989

WORLD-WIDE FLUCTUATIONS OF SARDINE AND ANCHOVY STOCKS: THE REGIME PROBLEM

D. LLUCH-BELDA[1], *R. J. M. CRAWFORD*[2], *T. KAWASAKI*[3], *A. D. MacCALL*[4], *R. H. PARRISH*[5], *R. A. SCHWARTZLOSE*[1,6] *and P. E. SMITH*[7]

Summed differences between the highest and lowest catches of two clupeoid taxa, sardines *Sardinops* spp. and *Sardina pilchardus* and anchovies *Engraulis* spp., in five regions where they co-occur are in excess of 29 million tons. Both taxa show large expansions and contractions of range with changes in abundance. Populations of sardines also shift alongshore, possibly in response to climate change. At time-scales of several decades, fluctuations in catches of sardines and anchovies are seemingly dominated by long-term environmental variations which cause large and prolonged changes in abundance and give rise to "regimes" of sardine or anchovy. These long-term fluctuations are probably associated with persistent environmental changes of oceanic to global scale, there being coherence of trends in various sardine stocks on an oceanic scale and similarities between these changes and global, hemispheric and oceanic indices of the environment.

Gesommeerde verskille tussen die hoogste en laagste vangs van twee klupeoïede taxa, sardyne *Sardinops* spp. en *Sardina pilchardus* en ansjovisse *Engraulis* spp., in vyf streke waar hul saam voorkom, oorskry 29 miljoen ton. Albei taxa vertoon groot uitbreidings en inkrimpings van verspreidingsgebied gepaardgaande met wisselings in talrykheid. Sardynbevolkings verskuif ook kuslangs, moontlik in reaksie op klimaatverandering. Op 'n tydskaal van etlike dekades word die skommelings van die sardyn- en ansjovisvangs blykbaar oorheers deur langtermynse omgewingsvariasies wat groot en langdurige veranderings in talrykheid veroorsaak en aanleiding gee tot "regimes" van sardyn of ansjovis. Hierdie langtermynse skommelinge hou waarskynlik verband met volgehoue omgewingsveranderings op 'n oseaan- tot wêreldskaal, want daar is samehang in die tendensies van verskeie sardynstapels op 'n oseaanskaal en ooreenkomste tussen hierdie veranderings en wêreld-, halfrond- en oseaan-indekse van die omgewing.

Varying catches of clupeoids contribute a disproportionate share of the total variability of the world harvest of fish. Two of the most important clupeoid groups commercially caught are sardines (*Sardinops* spp. and *Sardina pilchardus*) and anchovies (*Engraulis* spp.), which tend, in certain areas, notably those where tropical and subpolar currents mix, to coexist (Parrish *et al.* 1983, Kondô 1988). They share the important distinction of being able to digest carbohydrates, and are therefore able to feed on both phyto- and zooplankton (e.g. King and Macleod 1976, Kawasaki and Omori 1988) and to achieve high levels of abundance. The two taxa tend not to spawn in areas of intense offshore transport, where reproductive products may be lost from the shelf area, or in areas of strong turbulent mixing of the upper water column, where food patches may be disrupted (Parrish *et al.* op. cit.).

Intensive fisheries on sardines and anchovies are conducted in five regions of the world: the western (Japan system) and eastern (California Current) boundary areas of the North Pacific, the eastern boundary (Humboldt Current) of the South Pacific, and both the northern (Canary Current) and southern (Benguela system) boundaries of the eastern Atlantic. Both also co-occur off Australia (Blackburn 1967), but because they are generally not harvested there and data are consequently sparse, the Australian populations are not considered in this paper.

Maximum and minimum landings of sardines and anchovies in each of the five regions of intensive fishing until 1986 are listed in Table I. The pooled variation in catches of the two taxa amounts to more than 29 million metric tons, a figure which should be contrasted with the world harvest of about 80 million tons of marine fish in 1986 (F.A.O. 1988). Fortunately, the maxima and minima for the two taxa are not in phase, so fluctuations in the world harvest are damped.

The various populations of sardines and anchovies

1 Centro de Investigaciones Biologicas de Baja California Sur, AC La Paz, Baja California Sur, Mexico
2 Sea Fisheries Research Institute, Private Bag X2, Rogge Bay 8012, South Africa
3 Faculty of Agriculture, Tohoku University, Sendai, Japan
4 Tiburon Laboratory, Southwest Fisheries Center, NMFS, NOAA, Tiburon, California, U.S.A.
5 Pacific Fisheries Environmental Group, Southwest Fisheries Center, NMFS, NOAA, Monterey, California, U.S.A.
6 Scripps Institution of Oceanography, La Jolla, California, U.S.A.
7 Southwest Fisheries Center, NMFS, NOAA, La Jolla, California, U.S.A.

Manuscript received: May 1989

Table I: Variability of sardine and anchovy catches for the main fishery areas until 1986. The difference is obtained by subtracting the lowest catches from the highest catches in the historical record

Current/System	Maximum ('000 tons)	Minimum ('000 tons)	Difference ('000 tons)
Sardine			
Japan	5 191	9	5 182
California	719	12	707
Humboldt	5 814	0	5 814
Canary	1 096	3	1 093
Benguela	1 508	62	1 446
Anchovy			
Japan	474	28	446
California	424	0	424
Humboldt	13 060	59	13 001
Canary	836	0	836
Benguela	612	93	519

share many attributes, from their biology to the manner in which they are exploited and by which catches from them are utilized (e.g. Glantz 1983, Parrish *et al.* 1983, Crawford 1987, Silvert and Crawford 1988). Of particular interest, in view of their impact on the world fish harvest and on national economies, are the prolonged "regimes" of high or low abundance of the species (e.g. Glantz op. cit.). These regimes are of great importance to decision-making, especially that related to issues having implications over decades. In this paper, information on the regimes is synthesized and some factors that may influence their occurrence is discussed. Emphasis is placed on long-term population changes of sardines that have been observed worldwide.

CHANGES IN RANGE AND ABUNDANCE

Both sardines and anchovies have exhibited large expansions and contractions of range concomitant with changes in abundance. This statement is illustrated for the sardine in each of the five regions considered, taking the geographical extent of catches or information derived from spawning surveys or both to approximate the range, and the catches themselves as an index of abundance. Although catch alone is acknowledged to be a crude measure of abundance, direct surveys have only recently started in most systems, so there are no comparative indices for periods of high and low abundance from this method. Off South Africa, for example, estimates of population size from direct surveys are only available from 1983 onwards (Hampton 1987). Nevertheless, the changes in catches have been so marked (Table I) that there can be little doubt that they reflect real changes in population size (e.g. Chikuni 1985).

The Japan system

In the Japanese fishery, catches of sardine during periods of low abundance have been restricted to the south-eastern coasts of Kyushu, Shikoku and Honshu, and spawning to even smaller areas (Fig. 1a). During periods of high abundance, catches have been made around most of Japan, as well as off Korea, the maritime provinces of Siberia, and Sakhalin Island, and spawning has extended well into the Sea of Japan (Fig. 1b).

Sardine catches peaked around 1935, when landings exceeded 1,5 million tons. From the 1940s, however, catches decreased rapidly, and only 9 000 tons were caught in 1965 (Fig. 1c). Of note is the fact that the catch decreased during World War II, primarily because boats were requisitioned for military purposes. When the fleet was rebuilt after the war, catches remained low until the mid 1970s. There is general agreement that an unfavourable environment, rather than excessive exploitation, was the main cause of the decline (e.g. Hayasi 1983, Chikuni 1985, Kawasaki and Omori 1988). Catches increased rapidly again after 1975 and, in less than a decade, annual landings attained unprecedented levels of over five million tons (Fig. 1c). This recent proliferation of the sardine resource has taken place in spite of intense exploitation, and it has been attributed to a favourable environment (Kondo 1980, Kondô 1988, Kawasaki 1983, Kawasaki and Omori op. cit.).

Catches of the Japanese anchovy attained maximum levels of more than 400 000 tons in the 1960s and early 1970s. Thereafter, they decreased gradually while sardine catches were increasing rapidly (Fig. 1c, Hayasi 1967, 1983).

The California Current

Sardine formed the bulk of the purse-seine catch in the California Current from the mid 1930s to the mid 1940s. During this period of high abundance, catches were made along a large portion of the North American west coast, from British Columbia to southern Baja California (Fig. 2b). In the late 1970s, a period of lesser abundance, catches were confined mostly to the west coast of Baja California and the Gulf of California (Fig. 2a, Molina *et al.* 1987, Centro Interdisciplinario de Ciencias Marinas

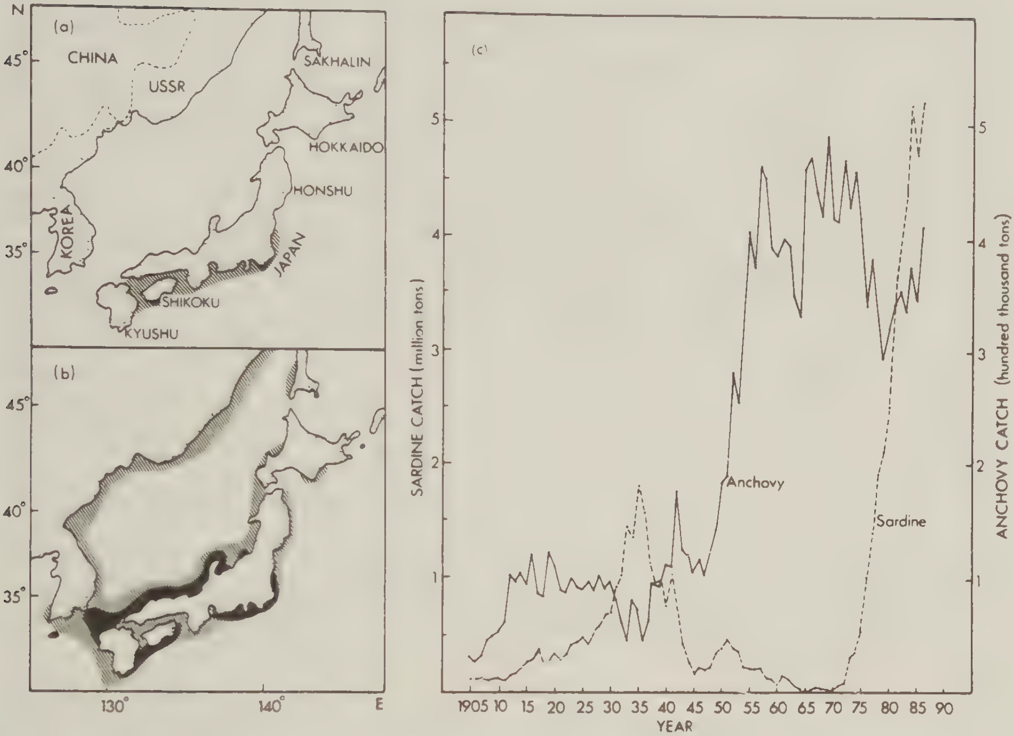


Fig. 1: Information pertaining to the Japanese sardine fishery (updated from Nakai 1959, Kawasaki and Omori 1988, and using information in Chikuni 1985, F.A.O. 1988) — fishing (hatched) and spawning (black) grounds during periods of (a) low and (b) high abundance, and (c) trends in the annual catches of sardine (dashed line) and anchovy (solid line)

[CICIMAR] unpublished data).

Sardine catches in the California Current peaked at over 700 000 tons in 1936, but they decreased rapidly between the mid 1940s and the early 1950s (Fig. 2c). Except for a small resurgence in 1958, they remained low until the mid 1970s, when catches off Baja California began to increase. From 1965 through 1985, the annual sardine catch off the United States state of California was <1 000 tons, and this was mostly a by-catch in the hauls of other species. In 1975 it was only 3 tons. Between 1966 and 1985 there was a moratorium on directed fishing for sardine off California (Troadec *et al.* 1980), but it was lifted in 1986 because estimates of biomass off California then exceeded the minimum (20 000 tons) above which fishing could again be allowed (Radovich 1982, Grant 1987). That year the total catch of sardines in the Gulf of California approached 300 000.

The decline of the Californian sardine, initiated in the 1940s, was evident first in the north and only later in the south. Ultimately, no sardine fisheries remained except off south-western Baja California and in the Gulf of California, the southern and near-tropical limits of the resource's distribution (Ramirez-Granados 1958, Radovich 1982, Pedrin-O. and Ancheita-Avalos 1976, Molina *et al.* 1987). In this southern region, sardine catches increased after 1975 (Molina *et al.* op. cit., CICIMAR unpublished data).

Anchovy catches off California and Baja California peaked between the mid 1970s and the early 1980s, over 340 000 tons being taken in 1981 (Fig. 2c). They then decreased substantially to slightly over 100 000 tons in the mid 1980s (Grant 1987, Cota-V. 1986, García-F. *et al.* 1986).

The Humboldt Current

Between 1963 and 1972, a period of low abundance of sardine in the Humboldt Current, the species

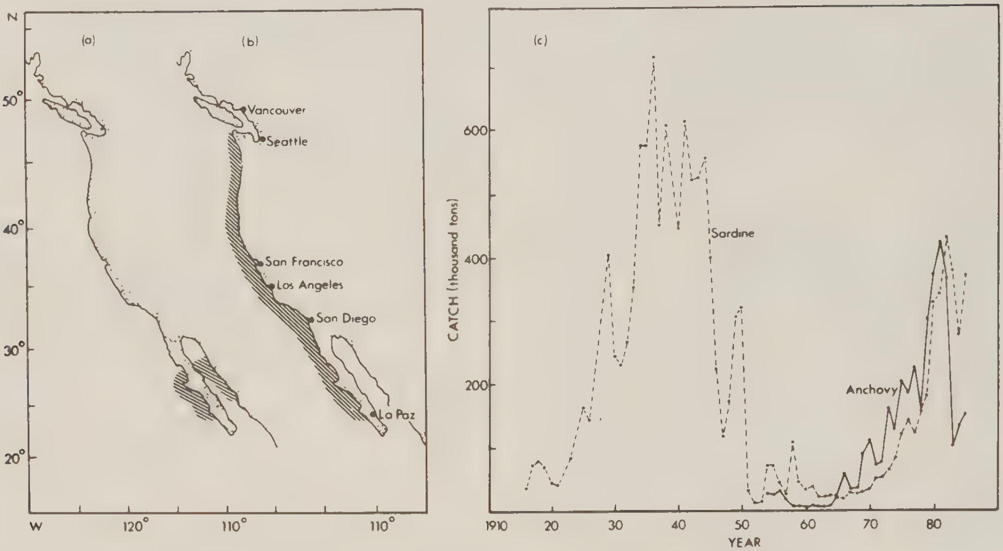


Fig. 2: Information pertaining to the sardine fishery of the California Current (catch data from Anon. 1961, Aasen 1967, Messersmith 1965, F.A.O. 1959–1984, F.A.O. 1988) — distribution during periods of (a) low and (b) high abundance, and (c) trends in annual catches of sardine (dashed line) and anchovy (solid line)

spawned off Chile only north of 27°S (Fig. 3a). Nine years later, when the population had grown considerably, substantial spawning was recorded in the Talcahuano region as far south as 40°S (Fig. 3b). Serra (1983) noted that no sardine were sampled in catches offloaded at Talcahuano in the late 1960s, and that several authors had indicated that the sardine's range did not extend south of Coquimbo (30°S) during the late 1950s and early 1960s. Off Peru, at the northern limit of the species' range, sardine were found as far north as 5°S in 1972, although at low density. A decade later, they extended to at least 3°S (the northern boundary of Peru), and considerable concentrations were to be found along the entire Peruvian coast (Zuta *et al.* 1983). In the mid 1960s, there was little spawning by sardines off Peru but, by the late 1970s and early 1980s, it was much heavier (Santander and De Castillo 1977, Muck *et al.* 1987).

The anchovy fishery off the west coast of South America started in the 1950s. It grew rapidly and catches peaked at more than 13 million tons in 1970, but it then declined even faster (Fig. 3c). In terms of yield, the decline was the most drastic in any fishery known to date (Yáñez-R. 1983, Zuta *et al.* 1983).

Sardine catches were low when the anchovy was abundant, but almost six million tons were taken in 1985 (F.A.O. 1988), the highest yield achieved to date by any of the world's sardine fisheries. It is clear also that sardine catches increased rapidly after the collapse of the anchovy resource.

The Canary Current

Off Morocco, sardines have been intensively exploited, but anchovy catches have been comparatively small. Both species have been fished extensively off the coasts of western and southern Europe. The near equatorial limits of sardines in the Canary Current are off Senegal, but extensions into the subarctic area include most of the region off western Europe (Garcia 1982, Belvèze and Erzini 1983, Riedel 1959, F.A.O. 1959–1984). In the English Channel near Plymouth, sardine eggs were abundant from the mid 1930s until about 1970, but not for periods of some 15 years on either side of this (Cushing 1982, Southward and Boalch 1988). Along the African coast, there was a considerable southward expansion of the sardine's range between 1966 and the mid 1970s, from Morocco to Senegal (Garcia op. cit.), with a subsequent retreat to the north (Gulland and Garcia 1984, Crawford and Shannon 1988, Fig. 4a, b). The expansion and contraction of the southern

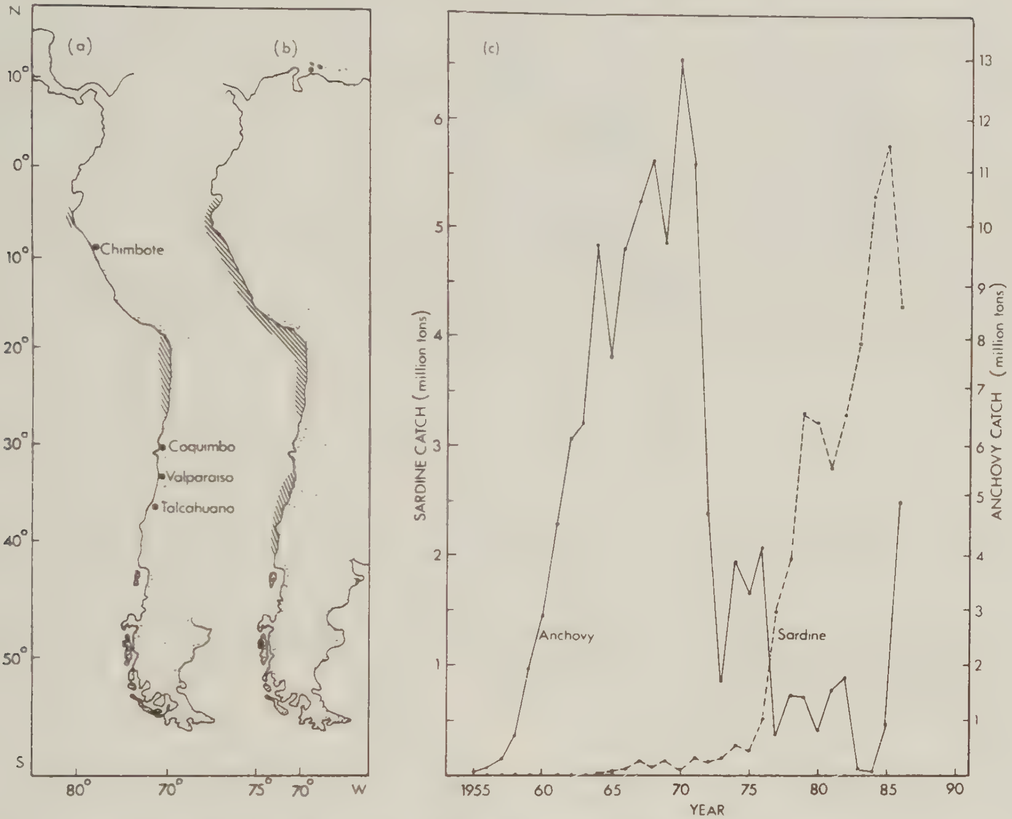


Fig. 3: Information pertaining to the sardine fishery of the Humboldt Current — spawning grounds during periods of (a) low and (b) high abundance (from information in Serra 1983, Santander and De Castillo 1977), and (c) trends in annual catches of sardine (dashed line) and anchovy (solid line)

limits corresponded with an estimated increase and decrease in the abundance of sardine there (Belvèze and Erzini op. cit.). The southward expansion also coincided with intensification of upwelling off Mauritania and Senegal (Binet 1988).

Catches of sardine in the Canary Current remained at moderate levels until the mid 1960s. They then climbed rapidly as the species extended its range southwards, and subsequently decreased with the species' retreat to the north (Fig. 4c).

The Benguela system

Purse-seiners exploit sardine (where it is locally known as pilchard) and anchovy in the Benguela system off both Namibia and South Africa. The results of tagging surveys and other information have indicated that relatively discrete stocks of both species exist north and south of an area of intense upwelling near Lüderitz, where the water is turbulent and cold (Crawford *et al.* 1988). During periods of reduced abundance, spawning has been restricted to the northern and south-eastern areas, but in years when the sardine has been plentiful, intensive spawning has also taken place nearer the centre of the system (Fig. 5a, b). Further, in years of apparently high biomass, catches have ranged considerably farther north off South Africa and south off Namibia than when biomass has been low (Crawford *et al.* 1987).

Purse-seine fisheries for sardine were initiated after World War II, and catches increased until 1968 (Armstrong and Thomas 1989). They then collapsed, stocks being at a very low level in the 1980s (Fig. 5c). Anchovy were not exploited before the mid 1960s,

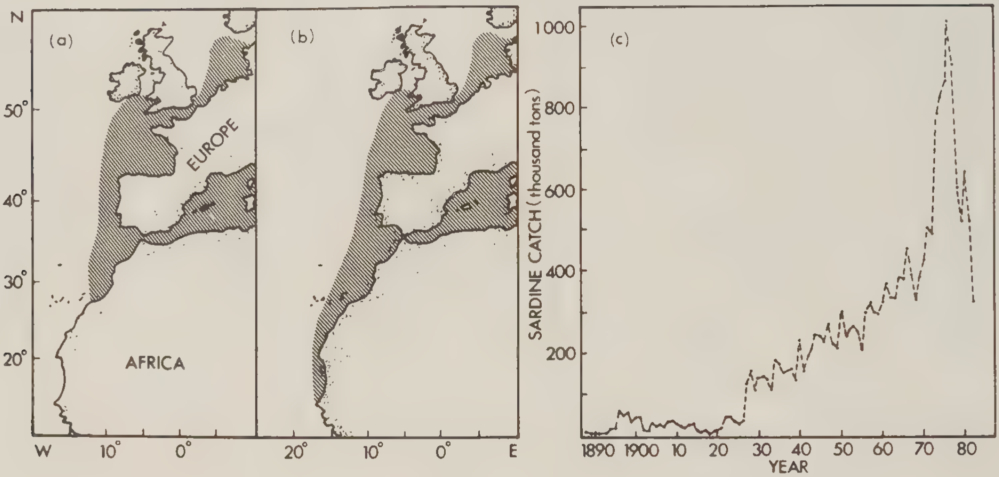


Fig. 4: Information pertaining to the sardine fishery of the Canary Current — distribution during periods of (a) low and (b) high abundance (from information in Garcia 1982), and (c) trends in annual catches of sardine

when small-meshed purse-seines were first permitted in the fishery. Thereafter, catches of anchovy increased concomitant with the decrease in sardine catches (Crawford *et al.* 1983, 1987).

DISCUSSION

Approximately parallel trends in sardine abun-

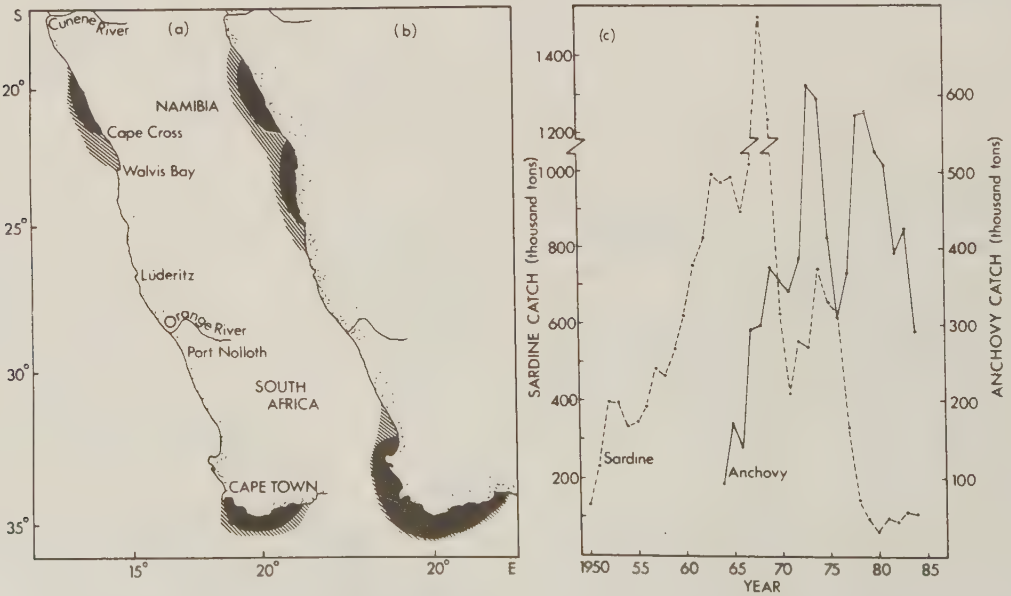


Fig. 5: Information pertaining to the sardine fishery of the Benguela system (based on information in Crawford *et al.* 1987) — major fishing (hatched) and spawning (black) grounds during periods of (a) low and (b) high abundance, and (c) trends in annual catches of sardine (dashed line) and anchovy (solid line)

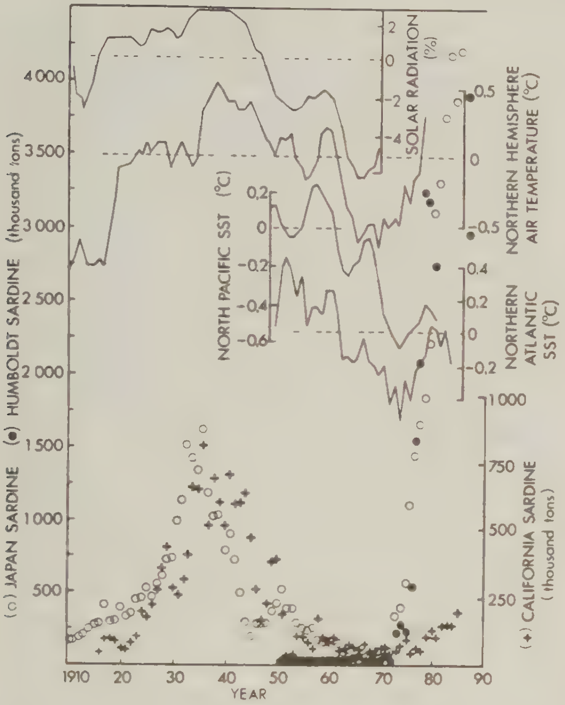


Fig. 6: Trends in anomalies of direct solar radiation (Miles 1978), air temperature for the northern hemisphere (from information in Raper *et al.* [1983] smoothed by five-year running means) and sea surface temperature for the North Pacific and North Atlantic (by courtesy D. Cayan, Scripps Institution of Oceanography, pers. comm.) compared with catches of sardine in the Japan (open circles), California (crosses) and Humboldt (dots) systems (updated from Kawasaki and Omori 1988)

dance in the Pacific Ocean have been documented by several authors (Kawasaki 1983, Kawasaki and Omori 1988). Catches off Japan and in the California Current were large in the 1930s and early 1940s, and then small until they began increasing again in both regions during the 1970s. Catches of sardine in the Humboldt Current were small until 1975, after which they also increased spectacularly. There was no fishing for sardine off Peru and Chile in the 1930s and 1940s, but in the early 1940s, the range of the sardine off Chile extended almost as far south as during the present period of high abundance (Serra 1983). It is therefore quite likely that sardine was also abundant in the Humboldt Current in the early 1940s.

Catches of sardines in the three regions of the Pacific are shown in Figure 6 together with indices of direct solar radiation (Miles 1978), air temperature for the northern hemisphere (Raper *et al.* 1983) and sea surface temperature for the North Pacific and North Atlantic (D. Cayan, Scripps Institution of Oceanography, pers. comm.). There is some similarity between the various time-series, maxima and minima occurring during the same general periods. Maxima are evident during the 1930s and 1940s and minima during the 1960s or early 1970s. Since then, each series has shown an upward trend. This approximate similarity is in spite of limitations inherent in the environmental data series. Insolation reaching the surface is influenced by cloud-cover and varies considerably from region to region, thereby complicating computation of a global mean and anomaly. Trends in air and sea surface temperature over large regions are also difficult to determine because the distribution of data is uneven.

Sardine abundance in the Atlantic Ocean is not in phase with that in the Pacific, and there is no apparent relationship between catches from the Canary Current as a whole and the mean sea surface temperature anomaly of the North Atlantic. However, near the United Kingdom, at the cool northern extremity of the sardine's range, there is some similarity between trends in catches and in sea surface temperature (Fig. 7). The period when sardine eggs were abundant in the English Channel coincided with above average sea temperatures there (Southward and Boalch 1988).

Sardines in each of the regions considered have shown a remarkable propensity to extend their range during periods of high abundance. In some of the regions, this has also held true for anchovy (e.g. MacCall 1984). Anchovy populations have tended to expand and contract about a fixed geographic centre (e.g. Fig. 8a, b), whereas sardines have tended to shift their geographic centre as well (e.g. Fig. 2a, b), often alongshore in response to climatic change.

The ranges of the sardine populations in the four eastern boundary currents have extended into cooler regions during warm periods. The Benguela system is unusual as an eastern boundary upwelling system in that it is bounded at both northern and south-eastern extremities by relatively warm water (Shannon 1985). Therefore, expansion into cooler regions has implied colonization of areas near the centre of the system. In the Humboldt, Canary and California currents as well as off Japan, range extensions into cooler regions have been polewards. In addition to its periodic colonization of cooler waters, the sardine of the Canary Current has expanded into a warmer southern area. There has also been an equatorward extension of the sardine's range in the South-East Pacific.

Sardines are more migratory than anchovies, and in some areas become increasingly so with age (see Murphy 1966). During periods of increasing abundance, sardines often expand their spawning areas upstream (e.g. Fig. 3a, b), thereby facilitating the advection of larvae to productive areas. El Niño events in the South-East Pacific and Benguela Niños in the South-East Atlantic may result in large, but temporary, shifts in the distribution of sardines, and they may therefore play an important role in the recolonization of upstream areas. As well as expanding their spawning range, sardines also extend their feeding range towards areas of high food productivity, whether upstream or downstream.

When their abundance is low, sardines contract into a few relatively fixed locations, and migratory behaviour is greatly reduced, though this may be caused partly by a shortened lifespan resulting from increased rates of mortality (e.g. Crawford 1981). In effect, at low levels of abundance, the geographic strategy of sardines becomes similar to that of anchovies.

It seems, therefore, that one consequence of intensively harvesting expanding or declining sardine stocks would be to reduce the lifespan and often, as a result, the migration range. A formerly self-perpetuating stock may well then collapse, thus prematurely shifting the population into a low-abundance mode.

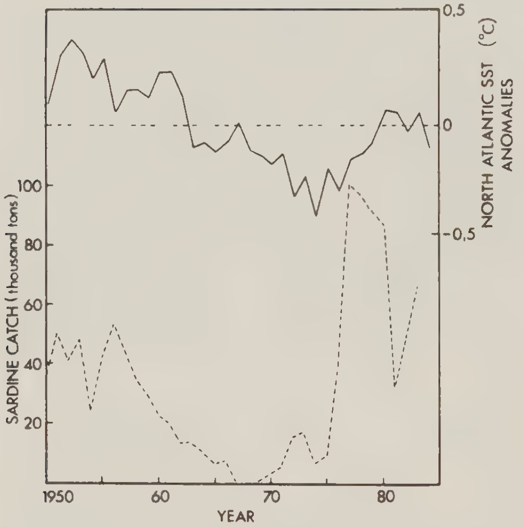


Fig. 7: An index of sea surface temperature anomaly for the North Atlantic (by courtesy D. Cayan, Scripps Institution of Oceanography, pers. comm.) compared with sardine catches off England

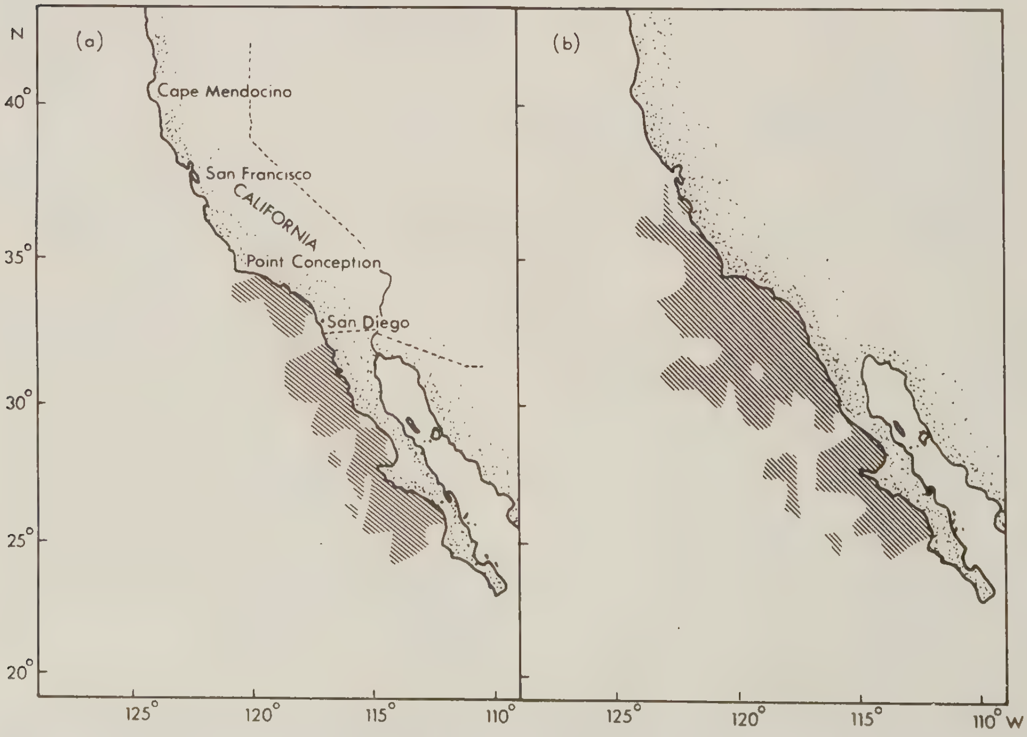


Fig. 8: Geographic distribution of anchovy larvae during periods of (a) low and (b) high abundance (after MacCall 1984)

This type of collapse has been experienced off both California and southern Africa (Murphy 1966, Crawford 1981). The Japanese sardine may be somewhat more resistant to overfishing, because advection of larvae and juveniles ensures that younger fish also participate in the geographic expansion of the species (e.g. Kondô 1988).

Short-term variability of sardine and anchovy populations, on time-scales of a few years, is undoubtedly influenced by environmental fluctuations (e.g. Shannon *et al.* 1988), and such variability tends to be amplified by exploitation. Fishery management can reduce fluctuations at intermediate time-scales by balancing harvests against stock productivity. However, longer-term fluctuations of sardine and anchovy resources seemingly again become unavoidably dominated by environmental variations which can cause large and prolonged changes in average stock productivity, giving rise to persistent regimes of high or low abundance of the species.

The mechanisms which initiate, sustain, and terminate outbursts of sardine or anchovy populations are not yet clear. If populations in widely separated areas are linked, as suggested by the coherence in trends of various sardine stocks on an oceanic scale (Fig. 6), the mechanisms must operate over similarly large spatial scales.

Long-term decisions, such as those pertaining to the scheduling of fleet replacement or the construction of processing plants, would be greatly facilitated by improved knowledge of the mechanisms underlying long-term fluctuations in sardine and anchovy populations or of the circumstances in which they occur. As short-term management of these populations is increasingly being based on measurement rather than prediction (e.g. Hampton 1987), a move away from the traditional "recruitment problem" to address the "regime problem" may prove to be a useful change in emphasis. As analysis of the regime problem would take less cognizance of ephemeral life stages and environments and more of long-term and large-scale averages and processes, it could well be more accessible to investigation than an analysis of the recruitment problem.

ACKNOWLEDGEMENTS

We thank the Centro de Investigaciones Biologicas de Baja California Sur, who hosted, in excellent manner, and covered the participants' expenses at the meeting at which this paper was developed. The travelling costs of RJMC were granted by the Benguela Ecology Programme of the South African National Committee for Oceanographic Research.

LITERATURE CITED

AASEN, K. D. 1967 — Review of the pelagic wet fisheries for the 1963-64, 1964-65, 1965-66 seasons. *Rep. Calif. coop. oceanic Fish. Invest.* **11**: 21-22.

ANON. 1961 — Review of the pelagic wet fisheries during the 1959-60 season. *Rep. Calif. coop. oceanic Fish. Invest.* **8**: 13-15.

ARMSTRONG, M. J. and R. M. THOMAS 1989 — Clupeoids. In *Oceans of Life off Southern Africa*. Payne, A. I. L. and R. J. M. Crawford (Eds). Cape Town; Vlaeberg: 105-121.

BELVÈZE, H. and K. ERZINI 1983 — The influence of hydroclimatic factors on the availability of the sardine (*Sardina pilchardus* Walbaum) in the Moroccan Atlantic fishery. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, April 1983*. Sharp, G. D. and J. Csirke (Eds). *F.A.O. Fish. Rep.* **291**(2): 285-327.

BINET, D. 1988 — Rôle possible d'une intensification des alizés sur le changement de répartition des sardines et sardinelles le long de la côte ouest africaine. *Aquat. Living Resour.* **1**: 115-132.

BLACKBURN, M. 1967 — Synopsis of biological information on the Australian anchovy *Engraulis australis* (White). *Rep. Calif. coop. oceanic Fish. Invest.* **11**: 34-43.

CHIKUNI, S. 1985 — The fish resources of the North-West Pacific. *F.A.O. Fish. tech. Pap.* **266**: 190 pp.

COTA-V., A. 1986 — Análisis de la pesquería de anchoveta, *Engraulis mordax* (Girard, 1857) mediante el uso de la composición por edad de la captura comercial para el periodo de 1957 a 1979. Tesis profesional, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, México.

CRAWFORD, R. J. M. 1981 — Distribution, availability and movements of pilchard *Sardinops ocellata* off South Africa, 1964-1976. *Fish. Bull. S. Afr.* **14**: 1-46.

CRAWFORD, R. J. M. 1987 — Food and population variability in five regions supporting large stocks of anchovy, sardine and horse mackerel. In *The Benguela and Comparable Ecosystems*. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 735-757.

CRAWFORD, R. J. M. and L. V. SHANNON 1988 — Long term changes in the distribution of fish catches in the Benguela. In *Long Term Changes in Marine Fish Populations*. Wyatt, T. and M. G. Larrañeta (Eds). Vigo; Instituto de Investigaciones Marinas de Vigo: 449-480 (Proceedings of a symposium held in Vigo, November 1986).

CRAWFORD, R. J. M., SHANNON, L. V. and D. E. POLLOCK 1987 — The Benguela ecosystem. 4. The major fish and invertebrate resources. In *Oceanography and Marine Biology. An Annual Review* **25**. Barnes, M. (Ed.). Aberdeen; University Press: 353-505.

CRAWFORD, R. J. M., SHANNON, L. V. and P. A. SHELTON 1988 — Characteristics and management of the Benguela as a large marine ecosystem. In *Biomass and Geography of Large Marine Ecosystems*. Sherman, K. and L. M. Alexander (Eds). American Association for the Advancement of Science: 171-221.

CRAWFORD, R. J. M., SHELTON, P. A. and L. HUTCHINGS 1983 — Aspects of variability of some neritic stocks in the southern Benguela system. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, April 1983*. Sharp, G. D. and J. Csirke (Eds). *F.A.O. Fish. Rep.* **291**(2): 407-448.

CUSHING, D. H. 1982 — *Climate and Fisheries*. London; Academic Press: 373 pp.

F.A.O. 1959 — Yearbook of fishery statistics. International trade, 1957. *F.A.O. Fish. Ser.* **8**.

F.A.O. 1959 — Yearbook of fishery statistics. Production and fishing craft, 1958. *F.A.O. Fish. Ser.* **9**.

F.A.O. 1960 — Yearbook of fishery statistics. International trade, 1958–59. *F.A.O. Fish. Ser.* **10**.

F.A.O. 1960 — Yearbook of fishery statistics. Production, 1959. *F.A.O. Fish. Ser.* **11**.

F.A.O. 1961 — Yearbook of fishery statistics. Production and fishing craft, 1960. *F.A.O. Fish. Ser.* **12**.

F.A.O. 1962 — Yearbook of fishery statistics. International trade, 1960–61. *F.A.O. Fish. Ser.* **13**.

F.A.O. 1962 — Yearbook of fishery statistics. Production, 1961. *F.A.O. Fish. Ser.* **14**.

F.A.O. 1963 — Yearbook of fishery statistics. Production and fishing craft, 1962. *F.A.O. Fish. Ser.* **15**.

F.A.O. 1964 — Yearbook of fishery statistics. Catches and landings, 1963, *F.A.O. Fish. Ser.* **16**.

F.A.O. 1965 — Yearbook of fishery statistics. Catches and landings, 1964. *F.A.O. Fish. Ser.* **18**.

F.A.O. 1966 — Yearbook of fishery statistics. Catches and landings, 1965. *F.A.O. Fish. Ser.* **20**.

F.A.O. 1967 — Yearbook of fishery statistics. Catches and landings, 1966. *F.A.O. Fish. Ser.* **22**.

F.A.O. 1968 — Yearbook of fishery statistics. Catches and landings, 1967. *F.A.O. Fish. Ser.* **24**.

F.A.O. 1969 — Yearbook of fishery statistics. Catches and landings, 1968. *F.A.O. Fish. Ser.* **26**.

F.A.O. 1970 — Yearbook of fishery statistics. Catches and landings, 1969. *F.A.O. Fish. Ser.* **28**.

F.A.O. 1971 — Yearbook of fishery statistics. Catches and landings, 1970. *F.A.O. Fish. Ser.* **30**.

F.A.O. 1972 — Yearbook of fishery statistics. Catches and landings, 1971. *F.A.O. Fish Ser.* **32**.

F.A.O. 1973 — Yearbook of fishery statistics. Catches and landings, 1972. *F.A.O. Fish. Ser.* **34**.

F.A.O. 1974 — Yearbook of fishery statistics. Catches and landings, 1973. *F.A.O. Fish. Ser.* **36**.

F.A.O. 1975 — Yearbook of fishery statistics. Catches and landings, 1974. *F.A.O. Fish Ser.* **38**. 374 pp.

F.A.O. 1976 — Yearbook of fishery statistics. Catches and landings, 1975. *F.A.O. Fish. Ser.* **40**: 417 pp.

F.A.O. 1977 — Yearbook of fishery statistics. Catches and landings, 1976. *F.A.O. Fish. Ser.* **42**: 320 pp.

F.A.O. 1978 — Yearbook of fishery statistics. Catches and landings, 1977. *F.A.O. Fish. Ser.* **44**: 343 pp.

F.A.O. 1979 — Yearbook of fishery statistics. Catches and landings, 1978. *F.A.O. Fish. Ser.* **46**: 358 pp.

F.A.O. 1980 — Yearbook of fishery statistics. Catches and landings, 1979. *F.A.O. Fish. Ser.* **48**: 384 pp.

F.A.O. 1981 — Yearbook of fishery statistics. Catches and landings, 1980. *F.A.O. Fish. Ser.* **50**: 386 pp.

F.A.O. 1982 — Yearbook of fishery statistics. Catches and landings, 1981. *F.A.O. Fish. Ser.* **52**: 357 pp.

F.A.O. 1983 — Yearbook of fishery statistics. Catches and landings, 1982. *F.A.O. Fish. Ser.* **54**: 393 pp.

F.A.O. 1984 — Yearbook of fishery statistics. Catches and landings, 1983. *F.A.O. Fish. Ser.* **56**: 393 pp.

F.A.O. 1988 — Yearbook of fishery statistics. Catches and landings, 1986. *F.A.O. Fish. Ser.* **62**: 479 pp.

GARCÍA-F., W., COTA-V., A., BARRERA-MORENO, A., FIGUEROA-L., J. A., LUÉVANO-B., A. and M. A. GRANADOS-G. 1986 — Resumen de la temporada de pesca comercial de anchoveta de 1984. *Documento téc. informativos Instituto nac. Pesca, México* **1**:77–101.

GARCIA, S. 1982 — Distribution, migration and spawning of the main fish resources in the northern CECAF area. *F.A.O. UNDP CECAF/ECAF series* **82/25**: 9 pp.

GLANTZ, M. H. 1983 — Man, state, and fisheries: an inquiry into some societal constraints that affect fisheries management. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, April 1983*. Sharp, G. D. and J. Csirke (Eds). *F.A.O. Fish. Rep.* **291**(3): 871–917.

GRANT, J. (Compiler) 1987 — Review of some California fisheries for 1986. *Rep. Calif. coop. oceanic Fish. Invest.* **28**: 11–20.

GULLAND, J. A. and S. GARCIA 1984 — Observed patterns in multispecies fisheries. In *Exploitation of Marine Communities*. May, R. M. (Ed.). Berlin; Springer: 155–190 (Report of the Dahlem Workshop on Exploitation of Marine Communities, Berlin, April 1984).

HAMPTON, I. 1987 — Acoustic study on the abundance and distribution of anchovy spawners and recruits in South African waters. In *The Benguela and Comparable Ecosystems*. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 901–917.

HAYASI, S. 1967 — A note on the biology and fishery of the Japanese anchovy *Engraulis japonica* (Houttuyn). *Rep. Calif. coop. oceanic Fish. Invest.* **11**: 44–57.

HAYASI, S. 1983 — Some explanation for changes in abundance of major neritic-pelagic stocks in the northwestern Pacific Ocean. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, April 1983*. Sharp, G. D. and J. Csirke (Eds). *F.A.O. Fish. Rep.* **291**(2): 37–55.

KAWASAKI, T. 1983 — Why do some pelagic fishes have wide fluctuations in their numbers? Biological basis of fluctuation from the viewpoint of evolutionary ecology. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, April 1983. Sharp, G. D. and J. Csirke (Eds). F.A.O. Fish. Rep.* **291**(3): 1065–1080.

KAWASAKI, T. and M. OMORI 1988 — Fluctuations in the three major sardine stocks in the Pacific and the global trend in temperature. In *Long Term Changes in Marine Fish Populations*. Wyatt, T. and M. G. Larrañeta (Eds). Vigo; Instituto de Investigaciones Marinas de Vigo: 37–53 (Proceedings of a symposium held in Vigo, November 1986).

KING, D. P. F. and P. R. MACLEOD 1976 — Comparison of the food and the filtering mechanism of pilchard *Sardinops ocellata* and anchovy *Engraulis capensis* off South West Africa, 1971–1972. *Investl Rep. Sea Fish. Brch S. Afr.* **111**: 29 pp.

KONDO, K. 1980 — The recovery of the Japanese sardine — the biological basis of stock-size fluctuations. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* **177**: 332–354.

KONDÔ, K. 1988 — Relationships between long term fluctuations in the Japanese sardine *Sardinops melanostictus* (Temmnick [*sic*] and Schlegel) and oceanographic conditions. In *Long Term Changes in Marine Fish Populations*. Wyatt, T. and M. G. Larrañeta (Eds). Vigo; Instituto de Investigaciones Marinas de Vigo: 365–392 (Proceedings of a symposium held in Vigo, November 1986).

MacCALL, A. D. 1984 — Population models of habitat selection, with application to the northern anchovy. *Administrative Report, Southwest Fisheries Center, La Jolla, California* **LJ-84-01**: 98 pp.

MESSERSMITH, J. D. 1965 — Review of the pelagic wet fisheries during the 1961–62 and 1962–63 seasons. *Rep. Calif. coop. oceanic Fish. Invest.* **10**: 8–9.

MILES, M. K. 1978 — Predicting temperature trend in the northern hemisphere to the year 2000. *Nature, Lond.* **276**(5686): 356–359.

MOLINA, D., PAEZ-B., F., CASTRO-F., A., MAGALLÓN-B., F., CASTRO-A., C. and J. ESTRADA-G. 1987 — Evolución de la pesquería de sardina en Guaymas, Son. Presentation at the 7th National Oceanographic Congress, Ensenada, Baja California, July 1987.

MUCK, P., SANDOVAL DE CASTILLO, O. and S. CARRASCO 1987 — Abundance of sardine, mackerel and horse mackerel eggs and larvae and their relationship to temperature, turbulence and anchoveta biomass off Peru. In *The Peruvian Anchoveta and its Upwelling Ecosystem: Three Decades of Change*. Pauly, D. and I. Tsukayama (Eds). *ICLARM Stud. Rev.* **15**: 268–275.

MURPHY, G. I. 1966 — Population biology of the Pacific sardine *(Sardinops caerulea)*. *Proc. Calif. Acad. Sci., Ser. 4* **34**(1): 1–84.

NAKAI, Z. 1959 — Changes in the population and catch of the Far East sardine area. In *Proceedings of the World Scientific Meeting on the Biology of Sardines and Related Species, Rome, September 1959*. **F.A.O./59/7/5496**: 22 pp. + 27 Figures and 9 Tables.

PARRISH, R. H., BAKUN, A., HUSBY, D. M. and C. S. NELSON 1983 — Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, April 1983*. Sharp, G. D. and J. Csirke (Eds). *F.A.O. Fish. Rep.* **291**(3): 731–777.

PEDRIN-O., A. O. and A. ANCHEITA-AVALOS 1976 — Estadisticas básicas de la explotación de sardina en el noroeste de México. *Serie informativos Instituto nac. Pesca, México* **INP-SI: i79**: 12 pp. + 27 Figures + 23 Tables.

RADOVICH, J. 1982 — The collapse of the California sardine fishery. What have we learned? *Rep. Calif. coop. oceanic Fish. Invest.* **23**: 56–78.

RAMIREZ-GRANADOS, R. 1958 — Aspectos biológicos y económicos de la pesquería de sardina *Sardinops caerulea* (Girard, 1954) en aguas mexicanas del Pacífico. Tesis profesional, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, México: 119 pp.

RAPER, S. C. B., WIGLEY, T. M. L., JONES, P. D., KELLEY, P. M., MAYES, P. R. and D. W. S. LIMBERT 1983 — Recent temperature changes in the Arctic and Antarctic. *Nature, Lond.* **306**(5942): 458–459.

RIEDEL, D. 1959 — European and Moroccan sardine production since 1920 off the Atlantic coast. In *Proceedings of the World Scientific Meeting on the Biology of Sardines and Related Species, Rome, September 1959*. **F.A.O./59/7/5494**: 8 pp. + 16 Figures and 11 Tables.

SANTANDER, H. and O. S. DE CASTILLO 1977 — Variaciones en la intensidad del desove de la sardina *Sardinops sagax sagax* (J) en la costa Peruana en los años 1966–1973. *Bol. Inst. Mar. Perú* **3**(3): 73–94.

SERRA, J. R. 1983 — Changes in the abundance of pelagic resources along the Chilean coast. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, April 1983*. Sharp, G. D. and J. Csirke (Eds). *F.A.O. Fish. Rep.* **291**(2): 255–284.

SHANNON, L. V. 1985 — The Benguela ecosystem. 1. Evolution of the Benguela, physical features and processes. In *Oceanography and Marine Biology. An Annual Review* **23**. Barnes, M. (Ed.). Aberdeen; University Press: 105–182.

SHANNON, L. V., CRAWFORD, R. J. M., BRUNDRIT, G. B. and L. G. UNDERHILL 1988 — Responses of fish populations in the Benguela ecosystem to environmental change. *J. Cons. perm. int. Explor. Mer* **45**(1): 5–12.

SILVERT, W. and R. J. M. CRAWFORD 1988 — The periodic replacement of one fish stock by another. In *Long Term Changes in Marine Fish Populations*. Wyatt, T. and M. G. Larrañeta (Eds). Vigo; Instituto de Investigaciones Marinas de Vigo: 161–180 (Proceedings of a symposium held in Vigo, November 1986).

SOUTHWARD, A. J. and G. T. BOALCH 1988 — Aspects of long term changes in the ecosystem of the western English Channel in relation to fish populations. In *Long Term Changes in Marine Fish Populations*. Wyatt, T. and M. G. Larrañeta (Eds). Vigo; Instituto de Investigaciones Marinas de Vigo: 415–447 (Proceedings of a symposium held in Vigo, November 1986).

TROADEC, J-P., CLARK, W. G. and J. A. GULLAND 1980 — A review of some pelagic fish stocks in other areas. *Rapp. P-v. Réun. Cons. perm. int. Explor. Mer.* **177**: 252–277.

YÁÑEZ-R., E. 1983 — Análisis de la pesquería pelágica de la zona de Coquimbo (30°S) realizada entre 1975 y 1980. In *Análisis de Pesquerías Chilenas*. Arana, P. (Ed.). Valparaiso; Universidad Católica de Valparaiso.

ZUTA, S., TSUKAYAMA, I. and R. VILLANUEVA 1983 — El ambiente marino y las fluctuaciones de las principales poblaciones pelágicas de la costa peruana. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, April 1983*. Sharp, G. D. and J. Csirke (Eds). *F.A.O. Fish. Rep.* **291**(2): 179–253.

8938

Precision and Bias of Estimates of Larval Mortality

Nancy C. H. Lo, John R. Hunter, and Roger P. Hewitt

ABSTRACT: The results of four ichthyoplankton surveys conducted during January through April 1984 off the coast of California were used as the basis for Monte Carlo simulation of populations of northern anchovy, *Engraulis mordax*, larvae. The simulated populations were sampled and larval mortality rate was calculated, using established analytical procedures. Results may be used to determine the precision of an estimate of larval mortality rate and to determine the number of plankton tows required to detect a difference in mortality rates between two surveys. The estimated mortality rate was found to be biased high when the larval growth rate is overestimated and biased low when the growth rate is underestimated. The bias is asymmetrically distributed and greatest when the assumed growth substantially overestimates the real growth. The results justify interannual comparisons of larval anchovy mortality rates when interannual variation in larval growth is less than twofold. The results also indicate that the sample size required for adequate precision of estimates of mortality rates is modest compared to that required for adequate representation of the spawning season and larval habitat.

The early life stages of several fish have been extensively studied as they are the link between the present adult stock and some future recruitment to the adult stock. Frustrated with the apparent lack of a clear relationship between stock and recruitment, fishery scientists have focused attention on events during the larval stage and their ultimate effect on survival to the juvenile and adult stages. Several hypotheses have been proposed (e.g., Hjort 1913); however, an understanding of the precision and accuracy of estimates of larval mortality rates is necessary to distinguish among them (Gulland 1971). This paper draws upon our experience with the northern anchovy, *Engraulis mordax*, to address this issue.

We focus on three questions: 1) What is the minimum number of plankton tows required to estimate the mortality rate of young larvae (<20 days old) for a given coefficient of variation? 2) What is the minimum number of plankton tows required to detect a difference in the mortality rates of young larvae between two surveys? 3) How does violation of the assumption of a constant growth model affect the estimate of larval mortality?

Several biases associated with sampling northern anchovy larvae have been identified and quantified. Pelagic ichthyoplankton are caught by lowering a fine-mesh net to a depth below the larval habitat and by steadily retrieving it to the surface of the ocean (Smith and Richardson 1977). Variability in the volume of water filtered per unit of depth affects the number of larvae captured; Ahlstrom (1948) formulated the "standard haul factor" to adjust for this bias. Larvae are extruded through the meshes of the sampling gear: retention rates can be expressed as a function of larval length and mesh size (Lenarz 1972; Zweifel and Smith 1981; Lo 1983). Larvae also evade capture as evidenced by differences in the night and day catch rates (Ahlstrom 1954; Smith 1981): retention rates can be expressed as a function of larval length and the diurnal time of capture (Hewitt and Methot 1982). The apparent length of larvae is affected by abrasion from the sampling net and by the preservative solution: live larval length may be expressed as a function of preserved larval length and the duration of the plankton tow (Theilacker 1980).

The application of these corrections yields unbiased estimates of the density of larvae in each of several length categories. Age-specific variations in growth introduce variability in the duration of time that a larva of given length is vulnerable to capture. The density of larvae divided by the duration of growth through each length category yields estimates of the number of larvae of a given age produced per unit sea-surface-area per unit time, which is termed larval production (Hewitt and Methot 1982). Yolk-sac larvae growth has been described as a function of temperature (Zweifel and Lasker

---

Nancy C. H. Lo, John R. Hunter, and Roger P. Hewitt: Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

Manscript accepted March 1989.
Fishery Bulletin, U.S. 87: 399–416.

1976; Lo 1983). Growth of feeding larvae has been described as a function of season (Methot and Hewitt 1980[1]). Interannual variations in growth have not been described, and in the absence of additional information, a larval growth model with constant coefficients is used for all years. The set of coefficients encompassed temperature effects as well as seasonal effects. The rate of decline of larval production with age represents the mortality rate (Hewitt 1981).

In actual practice, a negative binomial-weighted model (Bissel 1972) has been employed to convert length-specific distributions of larval density to unbiased age-specific distributions of larval production, assuming one set of size-specific extrusion and voidance rates (Zweifel and Smith 1981; Hewitt 1982; Hewitt and Methot 1982; Hewitt and Brewer 1983; Picquelle and Hewitt 1983, 1984; Lo 1985). The negative binomial distribution is recommended for describing sample counts of fish eggs and larvae (Smith and Richardson 1977); the distribution is capable of adequately describing patchy spatial distribution patterns. The arithmetic means of these distributions describe the mortality (or production) of larvae with age.

Although the negative binomial-weighted model produces an estimate of the variance of the mean density at a particular age, each age-specific distribution is unique because of the spatial dispersal of the larvae (Hewitt 1981). The variance of the mean density is underestimated as the extrusion and avoidance are assumed to be constant, and the variance about the mortality curve (hence, the variance of the mortality rate) is not easily determined. In the simulation, random variation of avoidance of the net and extrusion through the meshes of the net were included so that the variance of the mortality rate might best be evaluated. The approach used here is to construct a simulated population, sample it with simulated surveys, and estimate the mortality rate of larvae, using the procedures described above. By conducting many surveys, the accuracy and precision of the estimates of mortality rates may be investigated.

Potential biases in estimating larval mortality, introduced by assuming no interannual variation in growth, were our main concern and were investigated by simulation. Growth rates were varied when constructing the populations; mortality rates were subsequently calculated assuming a set of growth rates (i.e., no interannual variation). By comparing the calculated mortality rates to a known rate, the magnitude of biases may be investigated.

METHODS

A Monte Carlo simulation model (Fig. 1) was employed to address the questions pertaining to the biases and precision of the estimate of larval mortality. A population of anchovy larvae was constructed using observed seasonal and geographic distributions. A known mortality rate was imposed on the population and sampling effort was varied over time and space. Known sampling biases were imposed and then adjusted for using the same techniques for calculating larval mortality rate as have been used on real surveys. Several hundred simulated surveys were conducted to assess the accuracy and precision of the estimates of mortality rates. Simulated larval growth was also varied to determine the sensitivity of the estimates of mortality rates to an assumption of constant larval growth. The details of this simulation are outlined in the following paragraphs.

Larval Population

A series of CalCOFI[2] ichthyoplankton cruises conducted in 1984 (Fig. 2) was used as a basis for constructing the population of larvae in the ocean. The total abundance of anchovy larvae at each station was adjusted for extrusion of small larvae through the meshes of the net (Fig. 3) and avoidance of the net by large larvae (Fig. 4). The adjusted catches were then stratified by geographic region (Fig. 2), month, and temperature. The negative binomial distribution was fit to the observations (positive tows only) in each region-month-temperature cell owing to the patchiness of larvae and the fact that the mean larval abundance is less than the standard deviation in general (Table 1). Samples were randomly drawn from these distributions (where the variate was the total number of larvae <9.25 mm per station) to conduct a simulated survey.

---

[1] Methot, R. D., Jr., and R. P. Hewitt. 1980. A generalized growth curve for young anchovy larvae: derivation and tabular example. SWFC Admin. Rep. LJ-80-17, 8 p.

[2] California Cooperative Oceanic Fisheries Investigations (CalCOFI) is a consortium of marine institutions engaged in long-term monitoring and study of the pelagic ecology of the California Current. Large-scale ichthyoplankton surveys have been conducted since 1949. See Hewitt 1988, Reid 1988, and Smith and Moser 1988 for reviews.

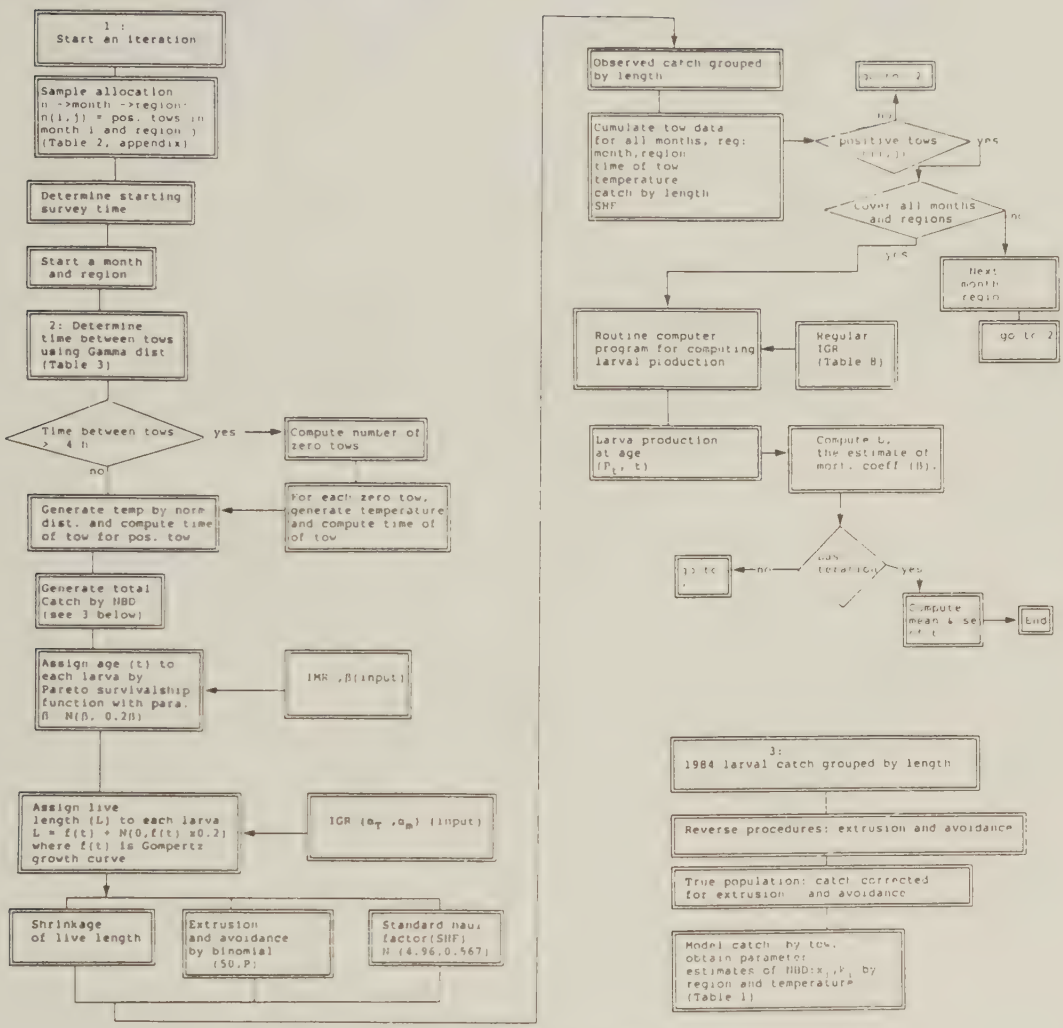

1 : Start an iteration
Sample allocation n ->month ->region: n(i,j) = pos. tows in month i and region j (Table 2, appendix)
Determine starting survey time
Start a month and region
2: Determine time between tows using Gamma dist (Table 3)
Time between tows > 4 h
yes
no
Compute number of zero tows
For each zero tow, generate temperature and compute time of of tow
Generate temp by norm dist. and compute time of tow for pos. tow
Generate total Catch by NBD (see 3 below)
Assign age (t) to each larva by Pareto survivalship function with para. β N(β, 0.2β)
IMR ,β(input)
Assign live length (L) to each larva L = f(t) + N(0,f(t) x0.2) where f(t) is Gompertz growth curve
IGR (a_T ,a_m) (input)
Shrinkage of live length
Extrusion and avoidance by binomial (50,P)
Standard haul factor(SHF) N (4.96,0.567)
Observed catch grouped by length
Cumulate tow data for all months, reg: month,region time of tow temperature catch by length SHF
positive tows (i,j)
no
go to 2
yes
cover all months and regions
no
Next month region
go to 2
yes
Routine computer program for computing larval production
Regular IGR (Table 8)
Larva production at age (P_t, t)
Compute b, the estimate of mort. coeff (B).
last iteration
no
go to 1
yes
Compute mean & se of b
End
3: 1984 larval catch grouped by length
Reverse procedures: extrusion and avoidance
True population: catch corrected for extrusion and avoidance
Model catch by tow, obtain parameter estimates of NBD:x, k, by region and temperature (Table 1)

FIGURE 1.—Flow chart of the simulation.

Allocation of Sampling Effort

Simulated population encountered by plankton tows was computed according to their distribution in 1984 by month and region (Table 1). The portion of simulated tows that contained anchovy larvae was similarly determined (Table 2; App.). In this way, the sample size (number of tows) could be varied and yet still retain the spatial and temporal distribution of sampling effort that was used in 1984. The time of the simulated tows was assigned by randomly selecting a value from a Gamma distribution fitted to the actual time between tows in each region (Table 3; App.).

Larval Mortality Rate

Because it was found that anchovy larvae suffer higher mortality during the first-feeding period than during later stages, a Pareto function describes the survival of anchovy larvae younger than 20 days adequately (Hewitt and Brewer 1983; Lo 1985, 1986). In the present study, we used the Pareto function to assign age to the larvae in the population (Table 1; Fig. 5; App.).

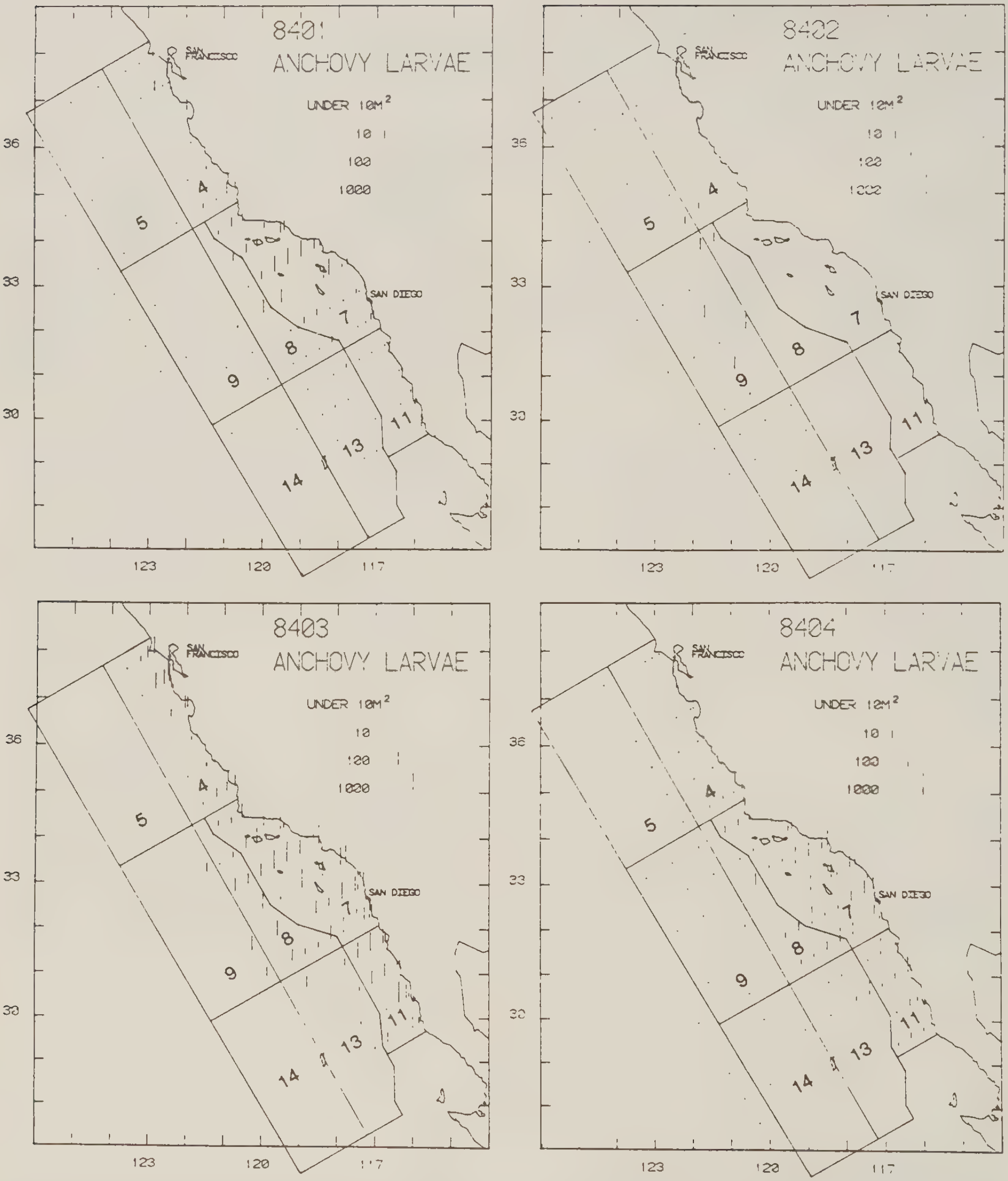


FIGURE 2.—Description of the seasonal and geographic distribution of sampling effort on a series of ichthyoplankton cruises conducted off the coast of California in 1984. The abundance of anchovy larvae at each station is indicated by the height of the "tree." Stations are grouped into geographic regions 4 through 14.

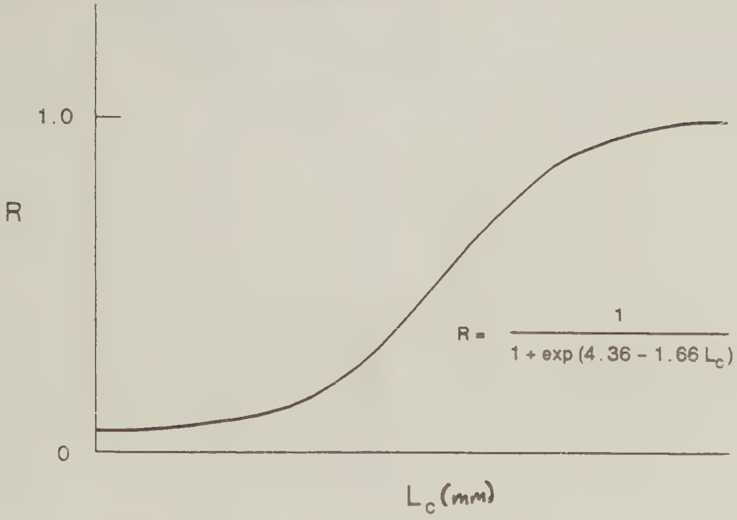
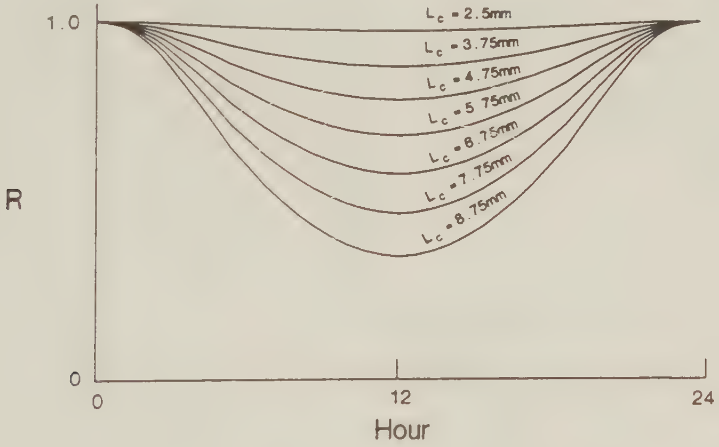


FIGURE 3.—Retention of anchovy larvae not extruded through the meshes of a plankton net constructed of 0.505 mm nylon (Lo 1983). R is the portion of larvae, of preserved length L_c, retained in the net.



$$R = \left(\frac{1 + DN_L}{2}\right) + \left(\frac{1 - DN_L}{2}\right) \cos\left(\frac{2\pi * \text{Hour}}{24}\right)$$

where:

L_c	DN_L
2.5	1.67
3.75	1.47
4.75	1.46
5.75	1.27
6.75	1.21
7.75	1.16
8.75	1.13

FIGURE 4.—Retention of anchovy larvae which have not avoided capture (Hewitt and Methot 1982). R is the portion of larvae, of preserved length L_c, retained in the net. DN_L is the length-specific day/night catch ratio.

TABLE 1.—Simulated population of anchovy larvae based on a series of ichthyoplankton surveys conducted in 1984. Tabulated values are the parameters (m and k) of negative binomial distributions[1] fit to the population stratified by month, region, and temperature.

		Temperature °C							
		≤13°		13.1°–14°		14.1°–15°		>15°	
Month	Region	m	k	m	k	m	k	m	k
1	4	31.25	0.39	63.00	0.34	27.50	0.51	27.50	0.51
	5	[2]0.25	∞	0.25	∞	0.25	∞	0.25	∞
	7	270.50	0.62	270.50	0.62	147.08	0.25	619.10	0.14
	8	2.00	∞	2.00	0.31	44.00	0.22	98.60	0.22
	9	34.00	0.60	34.00	0.60	136.00	0.41	51.00	4.33
	11	56.80	0.55	56.80	0.55	56.80	0.55	56.80	0.55
	13	6.80	0.37	6.80	0.37	6.80	0.37	6.80	0.37
	14	0.25	∞	0.25	∞	0.25	∞	0.25	∞
2	4	558.17	0.64	120.50	0.32	22.50	0.97	22.50	0.97
	5	0.25	∞	0.25	∞	0.25	∞	0.25	∞
	7	270.50	0.62	270.50	0.62	147.08	0.25	619.10	0.14
	8	2.00	∞	2.00	0.31	44.00	0.22	98.60	0.22
	9	34.00	0.60	34.00	0.60	136.00	0.41	51.00	4.33
	11	56.80	0.55	56.80	0.55	56.80	0.55	56.80	0.55
	13	6.80	0.37	6.80	0.37	6.80	0.37	6.80	0.37
	14	0.25	∞	0.25	∞	0.25	∞	0.25	∞
3	4	2.00	0.40	2.00	0.40	2.00	0.40	2.00	0.40
	5	0.25	∞	0.25	∞	0.25	∞	0.25	∞
	7	4.00	5.39	7.33	5.39	522.33	1.07	790.60	1.38
	8	117.50	0.50	117.50	0.50	520.00	0.20	206.30	0.45
	9	0.00	0.00	0.00	0.00	150.50	0.78	150.50	0.78
	11	14.50	2.14	14.50	2.14	147.00	1.22	514.30	0.45
	13	6.80	0.37	6.80	0.37	6.80	0.37	6.80	0.37
	14	0.25	∞	0.25	∞	0.25	∞	0.25	∞
	4	2.00	0.40	2.00	0.40	2.00	0.40	2.00	0.40
	5	0.25	∞	0.25	∞	0.25	∞	0.25	∞
	7	4.00	5.39	7.33	5.39	522.33	1.07	790.60	1.38
	8	117.50	0.50	117.50	0.50	520.00	0.20	206.30	0.45
	9	0.00	0.00	0.00	0.00	150.50	0.78	150.50	0.78
	11	14.50	2.14	14.50	2.14	147.00	1.22	514.30	0.45
	13	6.80	0.37	6.80	0.37	6.80	0.37	6.80	0.37
	14	0.25	∞	0.25	∞	0.25	∞	0.25	∞

[1] Negative binomial distribution where

$$P(X = x) = \frac{(x + k - 1)!}{x!(k - 1)!} * [m/m + k)]^x * [k/m + k)]^k \text{ for } x = 0,1,2,3,\ldots.$$

[2] Poisson distribution was used where $P(X = x) = (m^x e^{-m})/x!$ for $x = 0,1,2,3,\ldots.$

A two-step Gompertz growth curve (Fig. 6) was used to determine the corresponding larval length. The length at age was generated based on a normal distribution with mean equal to the length computed from the Gompertz growth curve and a standard deviation equal to 0.2 times the length. (The standard deviation is normally proportional to the mean length at age.) The coefficient of variation of 0.2 was arbitrarily chosen because no direct estimate of the standard deviation was available. These simulated larvae, with assigned ages and lengths, composed the catches.

Sampling Biases

The simulated catches were reduced to account for the effects of extrusion and avoidance.

TABLE 2.—Distribution of sampling effort during January through April 1984 by region and month, where $p(i)$ is the *proportion of tows for month i* and $\Sigma p(i) = 1$, $g(j|i)$ is the proportion of tows made in region j during month i and $\Sigma q(j|i) = 1$, and $r(j|i)$ is the proportion of positive tows for region j during month i and $0 \leq f(j|i) \leq 1$. The number of tows is indicated by N, and the positive tows are indicated by n (i.e., those tows which contained anchovy larvae)

	January		February		March		April		Total
$i =$	1		2		3		4		
$N =$	139		89		67		54		349
$n =$	55		55		47		19		176
$p(i)$	0.40		0.26		0.19		0.15		(0.50)
Region	q	r	q	r	q	r	q	r	
4	0.14	0.43	0.28	0.29	0	—	0.36	0.14	
5	0.14	0.06	0.20	0.06	0	—	0.15	0	
7	0.25	0.90	0.21	1.00	0.26	0.94	0.26	0.93	
8	0.04	0.67	0.01	1.00	0.14	0.88	0.02	1.00	
9	0.13	0.06	0.16	0.63	0.02	1.00	0.16	0.11	
11	0.14	0.33	0.06	0	0.24	0.88	0.05	0	
13	0.09	0.27	0.02	1.00	0.25	0.41	0	—	
14	0.07	0.08	0.06	0.17	0.09	0	0	—	
	1.00		1.00		1.00		1.00		

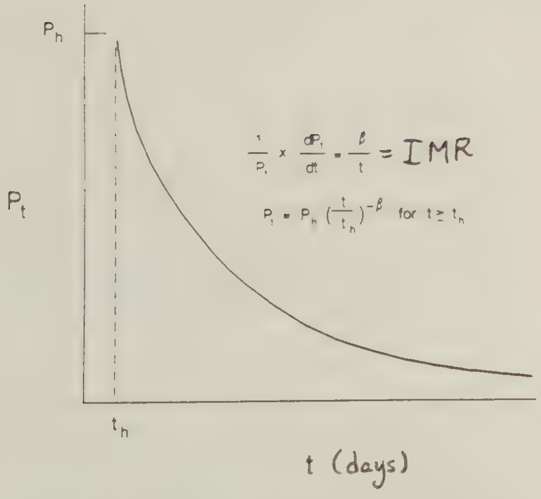


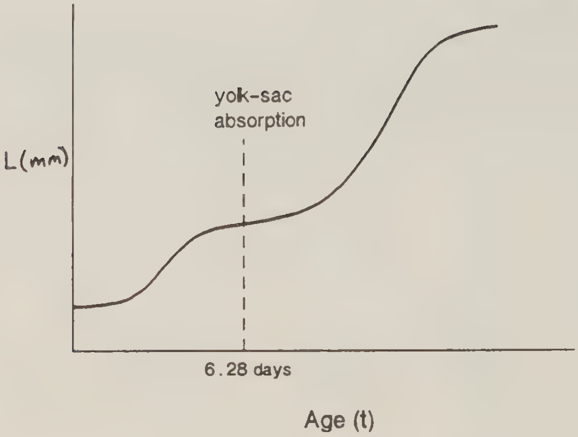
FIGURE 5.—Pareto model of larval production where larval mortality is assumed to decline with increasing age (Lo 1985 and 1986). P_t is the daily production of larvae at age t; β is the mortality coefficient; and t_h is the age at hatch.

TABLE 3.—Two parameters describing Gamma distributions[1] fit to the time between tows minus the constant in each region. Each of these distributions is shifted by the addition of the constant listed. The constant is the minimum time (hours) between two positive tows.

Regional	α	β	Constant
4	0.275	43.71	2
5	0.510	3.92	4
7	0.291	34.93	2
8	0.346	42.19	3
9	0.838	39.47	4
11	0.714	5.03	2
13	0.561	21.08	3
14	0.500	69.00	4

[1] Gamma distribution where

$$g(x) = \frac{1}{\beta(\alpha - 1)!} (x/\beta)^{-(\alpha-1)} \exp(-x/\beta) \text{ for } x > 0$$



$$L = 4.25 \left(\frac{0.32}{4.25}\right)^{e^{-\alpha_T t}} \quad \text{for } t \leq 6.28 \text{ days}$$

$$L = 27 \left(\frac{4.1}{27}\right)^{e^{-\alpha_m t}} \quad \text{for } t > 6.28 \text{ days}$$

$$\text{Where: } \alpha_T = a_T \exp(b_T \times \text{TEMPERATURE})$$

$$= 0.11 \exp(0.12 \times \text{TEMPERATURE})$$

$$\alpha_m = (a_m - b_m \times \text{MONTH})^{-1}$$

$$= (22.48 - 0.83 \times \text{MONTH})^{-1}$$

FIGURE 6.—Temperature-dependent and season-dependent larval growth curves (Methot and Hewitt 1980; Lo 1983). Gompertz models are used to describe each growth phase where α_T is the temperature-dependent growth coefficient and α_m is the season-dependent growth coefficient.

The fraction, p, of larvae extruded through the mesh or avoiding the net was generated by a sample mean of a binomial random variable, y, with parameters N and P. The parameter: N was set to 50 and P was the length-specific extrusion rate or avoidance rate from the same equations used to construct the population from the 1984 surveys. Thus p equaled $y/50$. Although p has a mean of P, it was not necessarily equal to P for each simulation run. The live lengths of larvae were reduced to account for the effects of net abrasion and preservaton effects (Theilacker 1980; Fig. 7). A standard haul factor was selected from the observed normal distribution of this variate (mean = 4.96, SD = 0.567) and used to index the volume of water filtered per unit of depth sampled. These catches then formed the raw material for the mortality estimation procedure.

Estimating Mortality Rate

The larvae in each catch were grouped into 1 mm length categories. A weighted negative binomial distribution was fitted to each length category where the original variate was the number of larvae (of a given length category) per station. Using this procedure, each observation was weighted for the effects of sampling biases (extrusion, avoidance, volume of water filtered, growth and shrinkage). The final variate was the number of larvae (of a given age) produced per day per 0.05 m^2 of sea surface. The rate at which larval production declines with time was defined as the mortality rate. For the Pareto model, the mortality rate was assumed to decline with age and mortality was indexed by the mortality coefficient (β). For the simulations described in this report, β was estimated as the slope of the log-

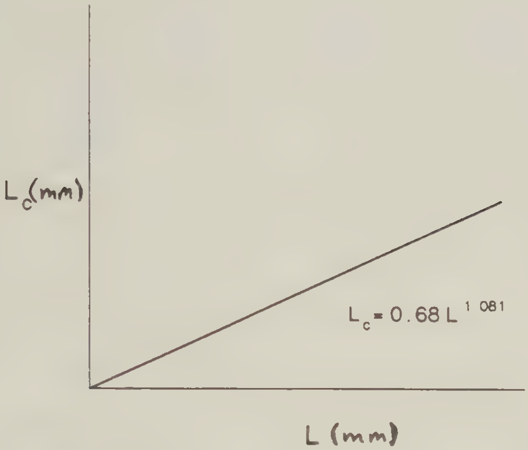


FIGURE 7.—The effect of net abrasion and preservative on the apparent length of anchovy larvae (from Theilacker 1980). L is live larval length; L_c is preserved (captured) larval length, and the length of the plankton tow is 20 minutes.

transformed Pareto function:

$$\ln(P_t) = \ln(P_h) - \beta \ln(t/t_h) .$$

Each simulation that produced an estimate of mortality rate was repeated many times. The collection of estimates of mortality rates was used to assess the accuracy and precision of estimates of mortality rates.

Sample Size for Detecting a Difference of Mortality Rates

The minimum sample size required to detect a difference between two mortalities was computed by two methods.

The *CV* Method

The coefficient of variation (cv) of the estimate of the difference between two mortality coefficients ($D = \beta_2 - \beta_1$) was calculated by

$$cv(d) = \frac{[\mathrm{var}(b_1) + \mathrm{var}(b_2)]^{0.5}}{D} \quad \text{for } D \neq 0 \qquad (1)$$

where d is the estimate of D, the difference between mortality coefficients β_1 and $\beta_2 (D = \beta_2 - \beta_1)$; b_1 and b_2 are the estimates of β_1 and β_2; $\mathrm{var}(b_1)$ and $\mathrm{var}(b_2)$ varying with sample size are computed in the simulation. The relationship between the sample size (n) and two elements, $cv(d)$ and D, enables us to determine the minimum sample size for a given $cv(d)$ and D.

The Power Method

The probability of detecting a difference in two mortality rates, given that there is a difference, was calculated as

$$P[d > c(\beta_1,n) \mid D] = P[Z > z(\beta_1,\beta_2,n)] \qquad (2)$$

where d follows a normal distribution with a mean of D and a variance of $[\mathrm{SE}(d)]^2$; Z follows a normal distribution with a mean of 0 and a variance of 1:

$$c(\beta_1,n) = 2\,\mathrm{SE}(d) = 2\sqrt{2}\,\mathrm{SE}(b) \quad \text{for } \beta_1 = \beta_2 (D = 0) \qquad (3)$$

$$z(\beta_1,\beta_2,n) = \frac{c(\beta_1,n) - D}{\mathrm{SE}(d)}$$

$$\text{and } \mathrm{SE}(d) = [\mathrm{var}(b_1) + \mathrm{var}(b_2)]^{0.5} \quad \text{for } \beta_2 \neq \beta_1 (D \neq 0).$$

A normal distribution table was used to obtain the probability values.

Relationship Between Growth and Mortality

The mortality coefficient (β) was fixed. Five populations were constructed with data from a single region-month stratum using five combinations of growth coefficients for yolk-sac (α_T, a temperature-specific coefficient) and feeding larvae (α_m, a season-specific coefficient) (see Table 8). Each population was sampled repeatedly and an average mortality coefficient calculated assuming standard growth coefficients. These mortality coefficients were then compared with the fixed mortality coefficient used to construct the populations.

RESULTS

The simulation model was used to estimate the following: 1) the mortality coefficients and their standard errors for various sample sizes when the true mortality coefficient was fixed, 2) the difference between two mortality coefficients and its standard error for various sample sizes, and 3) the mortality coefficients, assuming various growth rates.

Estimates of β with Various Sample Sizes

The mortality coefficient (β) was fixed at 1.5 for the inshore area (regions 4, 7, 8, 11, and 13; Fig. 2) and at 0.05 for the offshore area (regions 5, 9, and 14). The lower coefficient was required to generate simulated catch curves similar to those observed in offshore areas. The low mortality coefficient observed in offshore areas was likely the result of transport of older larvae from inshore to offshore regions (Power 1986). The average mortality coefficient (β), weighted by area of each region, was 1.41.

For each sample size (50, 100, 200, 300, and 400 plankton tows) 100 computer runs were made, and an estimate of the mortality coefficient (b) was calculated. The mean mortality coefficient, its standard error, and the coefficient of variation (cv) are listed in Table 4 for each sample size. The mean mortality coefficient for all sample sizes, except 50, slightly overestimated the true value of $\beta = 1.41$. The cv decreased with increasing sample size.

The relationship between cv and the number of positive tows (n) was quantified by assuming that half of the tows contained anchovy larvae (the actual portion of positive tows in 1984 was 0.5) (Table 2).The curve (Fig. 8) may be described by the power function:

$$cv(b) = 0.418\, n^{-0.47}$$

From Figure 8 and the above expression, cv may be expected to be 0.10, 0.06, or 0.05 for 20, 60, or 100 positive tows. For $n > 100$, cv may be expected to decrease at a slow rate. Thus a survey of 120 tows, yielding 60 positive tows, is sufficient to estimate the mortality coefficient with an expected $cv = 0.06$. Data from annual surveys conducted between 1980 and 1987, where the portion of positive tows ranged from 0.47 to 0.98, are also shown on Figure 8. The variation of b, as related to sample size during 1980–87, follows the relationship estimated from a single year's data and implies that the relationship can be used as a guide for sample size determination.

TABLE 4.—Mean, standard error (SE), and coefficient of variation (cv) of estimates of the mortality coefficient (b) for various sample sizes (N), with 50% positive for anchovy larvae (n = 0.5 N), from 100 computer runs of each simulated survey.

N	n	mean	SE	cv = SE/mean
50	25	1.39	0.13	0.09
100	50	1.43	0.09	0.06
200	100	1.44	0.06	0.04
300	150	1.44	0.06	0.05
400	200	1.43	0.05	0.03

Estimates of $\dot{D}$ with Various Sample Sizes

The mortality coefficient (β) was fixed at 1.0, 1.5, 2.0, 2.5, and 3.0 for the inshore area (regions 4, 7, 8, 11, and 13). The inshore area was relatively well sampled and contained relatively high abundances of larvae; the proportion of positive stations in these regions was approximately 0.6 (Tables 1, 2). Estimated mortality coefficients (b) were determined for five simulated populations (corresponding to each of the five mortality coefficients (β)) using sample sizes of 50, 100, and 200 plankton tows with 60% of them positive for anchovy larvae.

The average estimated mortality coefficient and its standard error were determined after 100 computer runs and listed in Table 5. As expected, standard errors decreased with increased sample size. The estimated mortality coefficient was biased slightly low for $\beta < 2$ and biased slightly high for $\beta > 2$. The biases are negligible although they appeared to increase in magnitude as β departed from 2. The estimates of mortality rates and their standard errors were used to determine minimum sample size by two methods.

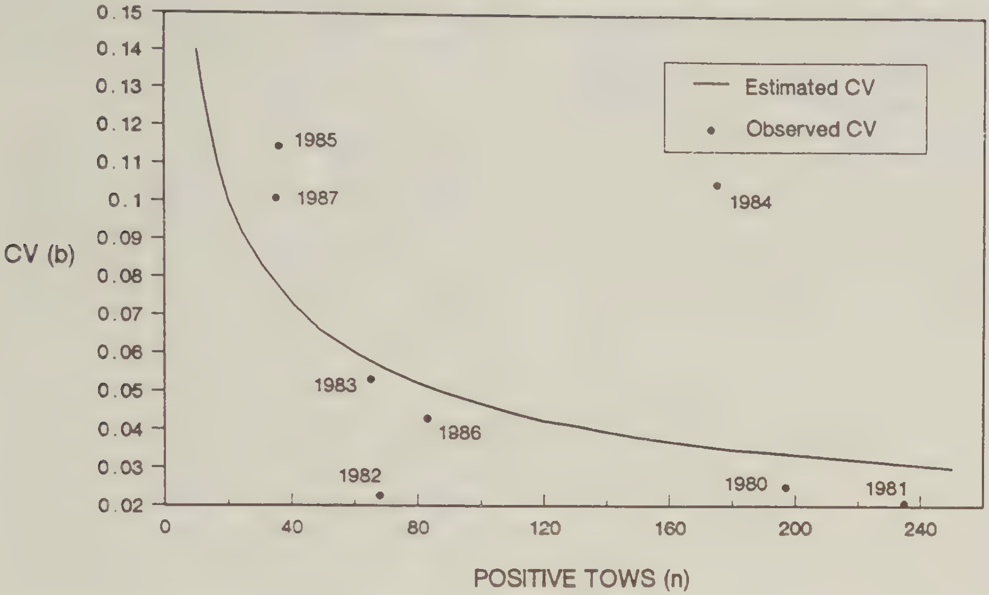


FIGURE 8.—The relationship between the coefficient of variation, cv(b), and the number of positive tows, n, derived from the results of the simulation. 1980–87 survey results are also plotted.

The *CV* Method

The *cv* of the estimate of the difference between two mortality coefficients, *cv(d)* (Equation (1)), was calculated for various mortality differences and sample sizes using the data listed in Table 5. The *cv(d)* decreases linearly with the difference between mortality coefficients (*D*), increases linearly with the absolute value of the larger of the two mortality coefficients (β_2), and exponentially declines with increasing sample size (*N*, *n*) (Table 6). The required sample size was thus estimated by regressing the number of positive tows on β_2, *D*, and $\ln[cv(d)]$:

$$n = -101 + 24.8\,\beta_2 - 150\,D - 128\ln[cv(d)]\,.$$

For example, estimating the difference between two estimated mortality coefficients, when the true mortality coefficients are 3.0 and

TABLE 5.—Mean and standard error (SE) of estimated mortality coefficient based on 100 computer runs. Five populations were simulated, each with a different mortality coefficient (β). Simulated surveys used three sample sizes (*N*) with 60% of the plankton tows positive for anchovy larvae (*n*).

	Sample size *N*(*n*)					
β	50(30)		100(60)		200(120)	
	mean	SE	mean	SE	mean	SE
1.00	0.90	0.100	0.91	0.075	0.93	0.058
1.50	1.44	0.090	1.44	0.064	1.44	0.060
2.00	1.98	0.120	1.99	0.087	2.01	0.058
2.50	2.56	0.110	2.57	0.097	2.58	0.065
3.00	3.18	0.170	3.18	0.100	3.18	0.075

TABLE 6.—Coefficient of variation of the estimate of the difference between two mortality coefficients, *cv*(*d*), calculated for various mortality differences, *D*, and sample sizes, *n*. The number of positive tows, *n*, was 60% of the total number of tows.

	Sample size *N*(*n*)		
$\beta_2 - \beta_1$	50(30)	100(60)	200(120)
D = 0.5			
1.5 − 1.0'	0.268	0.196	0.166
2.0 − 1.5	0.300	0.210	0.166
2.5 − 2.0	0.320	0.260	0.170
3.0 − 2.5	0.400	0.270	0.190
D = 1.0			
2.0 − 1.0	0.156	0.115	0.082
2.5 − 1.5	0.142	0.116	0.088
3.0 − 2.0	0.208	0.133	0.095
D = 1.5			
2.5 − 1.0	0.100	0.082	0.058
3.0 − 1.5	0.130	0.079	0.064

2.0 ($\beta_1 = 2.0$, $\beta_2 = 3.0$, $D = 1.0$), with a $cv(d) = 0.15$, will require $n = 67$ positive tows from each population. With 70 positive tows from each population, approximately 95% of the sample differences can be expected to be between 0.70 and 1.30 ($1.0 \pm 2 * 0.15$).

The Power Method

The standard error of the estimated mortality coefficient, SE(b), was modeled as a function of the number of positive tows, n, and the true mortality coefficient (β) using the data listed in Table 5:

$$\mathrm{SE}(b) = 0.356\, n^{-0.469}\, e^{0.239\beta}.$$

The probabilities of detecting a difference between two mortality coefficients, given that there is a difference (this is referred to as the power of the test), were calculated for various sample sizes and listed in Table 7. The power increases as the difference of mortality coefficients increases, and it is equal to the level of

TABLE 7.—Probability of detecting a difference between two mortality coefficients, given one of the mortality coefficients (β_1), the true difference ($D = \beta_2 - \beta_1$), and the number of positive tows (n). Because of symmetry about $D = 0$, partial figures are listed.

	True difference (D)							
n	−2.0	−1.5	−1.0	−0.5	0.5	1.0	1.5	2.0
$\beta_1 = 1.0$								
10					0.62	0.96	1.00	1.00
20					0.86	1.00	1.00	1.00
30					0.96	1.00	1.00	1.00
40					1.00	1.00	1.00	1.00
$\beta_1 = 1.5$								
10				0.50	0.50	0.97	1.00	
20				0.79	0.75	1.00	1.00	
30				0.93	0.90	1.00	1.00	
40				0.98	0.96	1.00	1.00	
50				1.00	0.99	1.00	1.00	
60				1.00	1.00	1.00	1.00	
$\beta_1 = 2.0$								
10			0.96	0.40	0.43	0.92		
20			1.00	0.70	0.70	1.00		
30			1.00	0.86	0.86	1.00		
40			1.00	0.93	0.92	1.00		
50			1.00	0.98	0.96	1.00		
60			1.00	1.00	1.00	1.00		
$\beta_1 = 2.5$								
10		1.00	0.91	0.34	0.48			
20		1.00	0.99	0.59	0.58			
30		1.00	1.00	0.76	0.75			
40		1.00	1.00	0.86	0.86			
50		1.00	1.00	0.93	0.91			
60		1.00	1.00	0.96	0.95			
70		1.00	1.00	1.00	1.00			
$\beta_1 = 3.0$								
10	1.00	0.99	0.82	0.27				
20	1.00	1.00	0.98	0.50				
30	1.00	1.00	1.00	0.66				
40	1.00	1.00	1.00	0.78				
50	1.00	1.00	1.00	0.86				
60	1.00	1.00	1.00	0.91				
70	1.00	1.00	1.00	0.95				
80	1.00	1.00	1.00	0.97				
90	1.00	1.00	1.00	1.00				

significance ($\alpha = 0.05$) when the difference is zero. The power is symmetrical about $D = 0$; thus, only partial figures were given in Table 7.

For example, if the true difference was 0.5 and one of the mortality coefficients was 2.0, with a probability of 0.86, a sample size of 30 positive tows from each of two populations will detect a significant difference in their mortality coefficients. The probability would be only 0.76 if one of the mortality coefficients was 2.5. In general, to achieve the same probability of detecting a given difference between mortality coefficients, a larger sample size is required for a larger β. To detect a significant difference with a probability of 0.96, when the true difference is 0.5 and one of the mortality coefficients is 1.0, 30 positive tows are required from each population. If $\beta = 2.5$, however, 60 positive tows are required to detect the same difference with a probability of 0.95. If the difference is greater than 1, at most 20 positive tows from each population would be sufficient.

The two methods serve different purposes. The *cv* method provides a 95% confidence interval for the difference. The Power Method assigns a probability to the detection of a difference, but provides no information on the magnitude of the difference.

Estimates of β with Various Growth Rates

Mortality is defined as the decline of production with larval age. Thus an overestimate of larval age, predicted from an underestimate of growth rate, will underestimate mortality rate. Similarly, an overestimate of growth rate will result in an overestimate of mortality rate.

The mortality coefficient (β) was fixed at 1.5. Data from February, region 7, temperature 15°C, were used to construct five populations, corresponding to five combinations of growth coefficients for yolk-sac and feeding larvae (Table 8). Each population was surveyed 50 times with a sample size of 50 plankton tows. The estimated mortality coefficient (b) was calculated by assuming standard growth coefficients for February, region 7, temperature 15°C (Table 8). When the population growth coefficients (α_m) were underestimated by the standard coefficients, the estimated mortality coefficient (b) was less than $\beta = 1.5$; conversely when growth was overestimated, the mortality coefficient was also overestimated.

Because the yolk-sac stage is short, relative to the feeding stage, we can reasonably assume that the growth coefficient for feeding larvae (α_m) has the largest effect on the estimated mortality coefficient (b). When the estimated mortality coefficient is plotted against α_m (Fig. 9), it is apparent that the bias in estimating mortality rate, caused by errors in the assumed growth rate, is asymmetrical: greater when actual growth is slower than assumed growth and smaller when actual growth is faster than assumed. When the actual growth was half the assumed rate, the mortality coefficient was overestimated by 80%; when the actual growth was double the assumed rate, the mortality coefficient was underestimated by only 16% (Table 8).

The coefficient, α_m, determines the instantaneous growth rate (IGR) at age t as the IGR = $\alpha_m \ln(L_\infty/L_0) \exp[-\alpha_m(t - t_0)]$ where L_∞ is the maximum fish length, and L_0 is the minimum fish length for $t > 6.28$ days (Fig. 6). Large value of α_m implies that the IGR is large for the small value of age t, and the IGR decreases rapidly as the fish ages. Because both the IGR and the instantaneous mortality rate (IMR = β/t) are two different nonlinear functions of age (t), the relationship between these two coefficients (α_m and β) is also nonlinear and thus the bias is asymmetric.

TABLE 8.—Five sets of coefficients for two-step Gompertz growth curves (Fig. 6) used to simulate five populations. Also listed are the standard coefficients used in the analysis of survey data for region 7 in February with a temperature of 15°C. The estimated mortality coefficient (b) is listed as average of 50 computer runs. The true mortality coefficient (β) was 1.5.

a_T	b_T	α_T	a_m	b_m	α_m	b
0.11	0.06	0.27	44.96	0.83	0.023	2.70
0.11	0.24	4.05	11.24	0.83	0.104	1.26
0.22	0.12	1.33	22.48	0.42	0.046	1.41
0.11	0.09	0.42	33.72	0.83	0.031	1.90
0.22	0.12	1.33	16.86	0.83	0.066	1.31
Standard coefficients:						
0.11	0.12	0.67	22.48	0.83	0.048	

DISCUSSION AND CONCLUSIONS

The simulation model and its methodology have general applicability to larval fish of many species, although these results apply directly to estimates of northern anchovy larval mortality rates derived from CalCOFI surveys. Results may differ because of differences in the param-

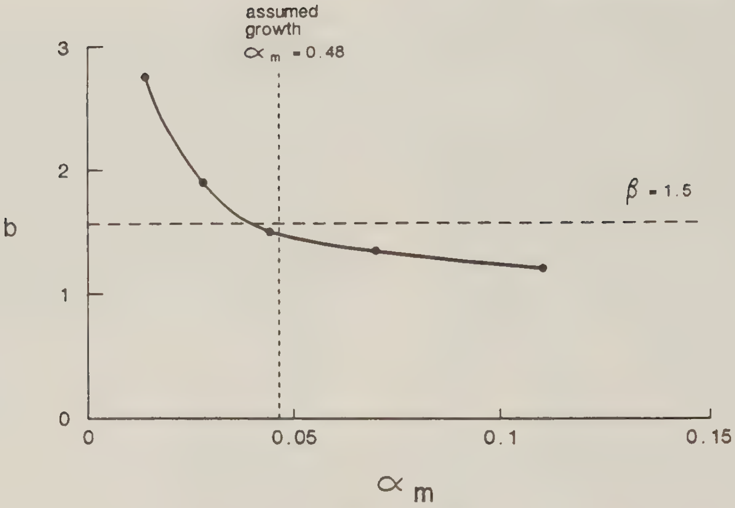


FIGURE 9.—The estimated mortality coefficient (b) is biased by errors in the assumed growth coefficient for feeding larvae, α_m = 0.48. The true mortality coefficient (β) was 1.5.

eter values and their variances. Nevertheless, most ichthyoplankton sampling problems are sufficiently similar so that the results derived for anchovy provide a general idea of the sample size required for adequate precision of larval mortality estimates. (When using the regressions derived in this study to estimate sample size, parameter values should be within the range used in the simulation [$1.0 \leq \beta \leq 3.0$, $0.5 \leq D \leq 2.0$]. Values outside these ranges could lead to unreliable estimates of sample size.) The results also provide an assessment of the effect of biased growth rates on estimates of larval mortality rate, which has general applicability to many species.

Caveats

Application to Site-Intensive Studies

Small-scale site-intensive studies may be conducted to study underlying mechanisms of larval mortality rate by measuring larval condition, growth, starvation rates, and mortality rate in small segments of the habitat. Such studies have greater problems with bias and precision than the CalCOFI surveys where the entire spawning habitat is sampled. As noted above, an important potential bias is the transport of larvae in or out of the study area. Taggart and Leggett (1987) noted that failure to account for advective losses of larvae from a small bay resulted in a significant overestimate of mortality.

Another problem arises from the choice of study areas. Many specimens must be collected over a short period to assess growth, starvation, and other condition factors. If sites are selected that contain larval densities that are high, relative to the average density for the entire habitat, and patchy, the effect will be to increase the variance, because the variance is often positively correlated with the density of larvae (Smith and Richardson 1977), and thereby reduce the power to detect differences in mortality rate between sites. The simulations were based on large regions of anchovy habitat and therefore underestimate sample size required to detect mortality rate differences between small areas of high larval abundance.

Application to Other Species

A key difference between larval anchovy and most other species of larval fishes is that anchovy are very abundant. The simulation results indicate that surprisingly few positive tows are needed to detect relatively small differences in mortality rates. In the regions considered in the simulation, 50–60% of the tows were positive, and the number of larvae caught per tow averaged 125, with 88% < 10 mm in length. For a less abundant species, the proportion of positive tows and the average number caught per tow would be much lower, and many more tows would be required to attain the same level of precision.

Application to CalCOFI Surveys

Three key assumptions underlie the use of the CalCOFI time series of larval mortality estimates for hypothesis testing: 1) a stable age distribution prevails (i.e., abundance of several cohorts of larvae at one moment in time is representative of one cohort as it ages through time), 2) variations in observed mortality rate represent true natural variations and not sampling error, and 3) use of the same larval growth parameters for all years does not bias the estimates of mortality rate.

The first assumption was not addressed in this study. It implies negligible immigration and emigration of larvae and continuous production of spawn. The CalCOFI surveys are designed to encompass the anchovy spawning habitat and thus minimize inaccuracies caused by transport of larvae in and out of the survey area. For a species with a broad temporal spawning curve and with repeated spawning by individuals (9–16% of the females spawn each night; table 7, Fiedler et al. 1986), unbiased estimates of mortality rate may be obtained by pooling plankton tows conducted throughout the spawning season (table 6, Hewitt and Methot 1982). With smaller surveys and shorter time periods, the assumption of a stable age distribution may not be suitable, and estimates of mortality rates may be biased.

With regard to the second assumption, our simulations indicate that the time series of daily mortality rate of anchovy larvae represents predominantly real differences owing to biological variation rather than random variation. Recent CalCOFI ichthyoplankton surveys (Table 9) yielded between 36 and 236 positive tows per spawning season. The simulation model indicates that sample sizes >80 are sufficient to detect a difference of 0.5 or more in the mortality coefficient (β) between years (Table 7). When all possible pairs for the eight surveys (1980–87) are compared, 12 of the 28 comparisons had a difference >0.5 (Table 9). Results of our simulation imply that the precision of past surveys was adequate, and the interannual variation in mortality rate (β ranged from 1.22 in 1980 to 2.14 in 1986) is real.

Because larval mortality rate is age-dependent (IMR = β/*t*) with high mortality occurring during the onset of feeding and decreasing thereafter, variations in daily mortality rates can be typified by "large differences concentrated in a short period of time" and thus be easily detectable (Gulland 1971). The critical issue in comparing mortality rates does not appear to be one of precision but rather one of obtaining a representative sample.

With regard to the third assumption, the simulation also indicated that the risk of introducing a large bias in estimates of mortality rates by using a single family of standard growth curves is relatively low. A large bias would be expected only when the standard growth curves overestimated the actual growth by a factor of two or more. It is unknown how frequently the standard growth curve generates this large bias, for lack of data on variability of larval growth rates from year to year in the field.

TABLE 9.—Number of tows positive for anchovy larvae (*n*) and mortality coefficients (β) for CalCOFI ichthyoplankton surveys conducted during January through April 1980–87.

Year	*n*	β
1980	197	1.22
1981	236	1.53
1982	69	1.81
1983	65	2.05
1984	176	1.47
1985	37	2.03
1986	83	2.14
1987	36	1.98

CONCLUSIONS

These simulations validate the use of CalCOFI survey information to test hypotheses regarding larval survival and recruitment (Butler 1987, Peterman et al. 1988). The sample size required for adequate precision of estimates of mortality rates is modest relative to the one required for adequate representation of the spawning season and habitat of a major marine stock such as the northern anchovy. As stated, the critical issue in comparing mortality rates does not appear to be precision of the estimates but rather how well the sample represents the population.

ACKNOWLEDGMENTS

We would like to acknowledge Paul Smith, who outlined the main consideration necessary to calculate the mortality of young anchovies; James Zweifel, who developed the methods to do it; two referees for their critical reviews; and most of all Dr. Reuben Lasker, who encouraged all of us.

LITERATURE CITED

Ahlstrom, E.

1948. A record of pilchard eggs and larvae collected during surveys made in 1939 to 1941. U.S. Fish. Wild. Serv. Spec. Sci. Rep. 54, 82 p.

1954. Distribution and abundance of egg larvae populations of the Pacific sardine. U.S. Fish Wildl. Serv., Fish. Bull. 93:83–140.

Bissel, A. F.

1972. A negative binomial model with varying element sizes. Biometrika 59:435–441.

Butler, J.

1987. Comparison of the larval and juvenile growth and larval mortality rates of Pacific sardine and northern anchovy and implications for species interaction. Ph.D. Thesis, Univ. California at San Diego, 242 p.

Fiedler, P. C., R. D. Methot, and R. P. Hewitt.

1986. Effects of California El Nino 1982–1984 on the northern anchovy. J. Mar. Res. 44:317–338.

Gulland, J. A.

1971. Ecological aspects of fishery research. Adv. Ecol. Res. 7:115–176.

Hewitt, R. P.

1981. The value of pattern in the distribution of young fish. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:229–236.

1982. Spatial pattern and survival of anchovy larvae: implications of adult reproductive strategy. Ph.D. Thesis, Univ. California at San Diego, 187 p.

1988. Historical review of the oceanographic approach to fishery research. CalCOFI Rep. 29:27–41.

Hewitt, R. P., and G. D. Brewer.

1983. Nearshore production of young anchovy. CalCOFI Rep. 24:235–244.

Hewitt, R. P., and R. D. Methot, Jr.

1982. Distribution and mortality of northern anchovy larvae in 1978 and 1979. CalCOFI Rep. 23:226–245.

Hjort, J.

1913. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-v. Réun. Cons. int. Explor. Mer 19:1–228.

Lenarz, W. H.

1972. Mesh retention of *Sardinops caerulea* and *Engraulis mordax* by plankton nets. Fish. Bull. U.S. 70:839–848.

Lo, N. C. H.

1983. Re-examination of three parameters associated with anchovy egg and larval abundance: temperature dependent incubation time, yolk-sac growth rate and egg and larval retention in mesh nets. NOAA Tech. Memo. NMFS-SWFC-31, 32 p.

1985. Egg production of the central stock of northern anchovy 1951–83. Fish. Bull. U.S. 83:137–150.

1986. Modeling life-stage-specific instantaneous mortality rates, an application to northern anchovy, *Engraulis mordax*, eggs and larvae. Fish. Bull. U.S. 84:395–407.

Peterman, R. M., M. J. Bradford, N. C. H. Lo, and R. D. Methot, Jr.

1988. Contribution of early life stages to interannual variability in recruitment of northern anchovy (*Engraulis mordax*). Can. J. Fish. Aquat. Sci. 45(1):8–16.

Picquelle, S. J., and R. P. Hewitt.

1983. The northern anchovy spawning biomass for the 1982–83 California fishing season. CalCOFI Rep. 24:16–28.

1984. The 1983 spawning biomass of the northern anchovy. CalCOFI Rep. 25:16–27.

Power, J. H.

1986. A model of the drift of northern anchovy, *Engraulis mordax*, larvae in the California Current. Fish. Bull. U.S. 4:585–603.

Reid, J. L.

1988. Physical oceanography 1947–1987. CalCOFI Rep. 29:42–65.

Smith, P. E.

1981. Fisheries on coastal pelagic schooling fish. *In* R. Lasker (editor), Marine fish larvae: morphology, ecology, and relation to fisheries, p. 1-30. Univ. Wash. Press., Seattle.

Smith, P. E., and H. G. Moser.

1988. CalCOFI time series: An overview of fishes. CalCOFI Rep. 29:66–78.

Smith, P. E., and S. Richardson.

1977. Standard techniques for pelagic fish egg and larva surveys. F.A.O. Fish. Tech. Pap. 175, 100 p.

Taggart, C. T., and W. C. Leggett.

1987. Short-term mortality in post-emergent larval capelin *Mallotus villosus*. I. Analysis of multiple *in situ* estimates. Mar. Ecol. Prog. Ser. 41, p. 205–217.

Theilacker, G. M.

1980. Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservative. Fish. Bull., U.S. 78:685–692

Zweifel, J., and R. Lasker.

1976. Prehatch and posthatch growth of fishes—a general model. Fish. Bull., U.S. 74:609–622.

Zweifel, J. R., and P. E. Smith.

1981. Estimates of the abundance and mortality of larval anchovies (1951–1975): application of a new method. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:248–259.

APPENDIX

Assignment of Larval Ages Using the Pareto Function

The standing stock (SS) of larvae, between the ages of t_h and 20 days, is the integral of the production curve (Fig. 5) over these ages:

$$SS = \int_{t_h}^{20} P_t \, dt = \int_{t_h}^{20} P_h(t/t_h)^{-\beta} dt$$

$$= [1 - (20/t_h)^{-(\beta-1)}] \frac{t_h P_h}{(\beta - 1)} \qquad \text{for } \beta < > 1,$$

$$= [\ln(20) - \ln(t_h)] t_h P_h \qquad \text{for } \beta = 1.$$

Similarly the number of larvae younger than age t is

$$SS_t = [1 - (t/t_h)^{-(\beta-1)}] \frac{t_h P_h}{(\beta - 1)} \qquad \text{for } \beta < > 1,$$

$$= [\ln(t) - \ln(t_n)] \, t_h P_h \qquad \text{for } \beta = 1.$$

The proportion of larvae that are younger than age t is

$$r(t) = SS_t/SS = \frac{1 - (t/t_h)^{-(\beta-1)}}{1 - (20/t_h)^{-(\beta-1)}} \qquad \text{for } \beta <> 1,$$

$$= \frac{\ln(t/t_h)}{\ln(20/t_h)} \qquad \text{for } \beta = 1,$$

where $0 < r(t) < 1$.

By rearranging terms, t can be expressed as

$$t = t_h[1 - r(t)(1 - (20/t_h)^{-(b-1)}]^{-1/(b-1)} \qquad \text{for } b <> 1,$$

$$= t_h(20/t_h)^{r(t)} \qquad \text{for } b = 1,$$

where b is a normal random variable with mean = β and standard error = 0.2 β (0.2 is an arbitrarily chosen value for the coefficient of variation (b) and $r(t)$ is a uniform random variable between 0 and 1).

Sample Allocation

The allocation of tows to each region and month was based on the 1984 sampling pattern (Table 2, Fig. 2). For a total of N tows, the number of positive tows allocated to month i and region j was computed as

$$n(i,j) = N * p(i) * q(j|i) * r(j|i)$$

where $p(i)$ is the proportion of tows for month i and $\Sigma p(i) = 1$
$q(j|i)$ is the proportion of tows made in region j during month i and $\Sigma q(j|i) = 1$
$r(j|i)$ is the proportion of positive tows for region j during month i and $0 < = r(j|i) < = 1$.

A uniform random number generator was used to assign each tow to a month and region, to determine whether the tow was positive or not, and thus to produce $n(i,j)$.

Assignment of the Time of Tow

Table 3 lists parameters for Gamma distributions fitted to the actual time between positive tows minus the minimum time between any two positive tows (i.e., plankton tows which caught at least one anchovy larva) in each region because the Gamma distribution takes all values to be greater than zero. Each distribution is shifted to the right by the constant listed (the minimum time between any two positive tows). Actual times greater than 150 hours were assumed to be periods of transit to and from port and were thus excluded when fitting the distributions.

The time of the first tow of a simulated survey was chosen randomly and incremented by time intervals selected from the distributions described in Table 3. If the selected time interval was greater than 4 hours, tows with zero catch were inserted. The number of zero tows inserted was the time interval between two positive stations divided by the average travel time between stations (2 hours).

8939

SPAWNING BIOMASS OF THE NORTHERN ANCHOVY IN 1988

NANCY C. H. LO
National Marine Fisheries Service
Southwest Fisheries Center
P.O. Box 271
La Jolla, California 92038

RICHARD D. METHOT
Northwest and Alaska Fisheries Center
7600 Sand Point Way N.E.
Seattle, Washington 98115

ABSTRACT

The spawning biomass estimate of the northern anchovy in 1988 is 1,009,000 MT. The estimate was made with the stock synthesis (SS) model, which uses time series of abundance data and age composition data, anchovy landings from the United States and Mexico, and sea-surface temperature. New data incorporated in the 1988 estimate were an egg production index derived from CalCOFI plankton samples of January–February 1988, monthly sea-surface temperatures taken at the pier of the Scripps Institution of Oceanography, and the age composition from the Mexican fishery in Ensenada during 1987. The spawning biomass of anchovy in 1988 remained at a level similar to that in 1987.

RESUMEN

La estimación de la biomasa del desove de la anchoveta del norte es de 1,009,000 toneladas métricas para 1988. Esta estimación se realizo por medio del modelo de síntesis del stock ("stock synthesis", SS), que utiliza una combinación de datos distribuídos en el tiempo de abundancia y composición por edad, datos de desembarque de capturas de los Estados Unidos y Mexico, y datos de temperatura de la superficie del mar. Se incorporaron a la estimación de la biomasa del desove para 1988 datos nuevos, tales como el índice de producción de huevos obtenido de las muestas de plancton recolectadas en los meses de enero y febrero de 1988 por la campaña de la CalCOFI, los valores de temperatura de las aguas de superficie obtenidos desde el muelle del Scripps Institution of Oceanography, y los datos de composición por edad obtenidos por la pesquería de Ensenada durante el año 1987. La biomasa del desove de la anchoveta para 1988 es similar a la del año 1987.

INTRODUCTION

This is a report on the estimate of the 1988 spawning biomass of the central subpopulation of the northern anchovy (*Engraulis mordax*). The Southwest Fisheries Center is required to estimate the spawning biomass according to the provisions of the Anchovy Management Plan of the Pacific Fishery Management Council (PFMC 1983). In 1980–85, the spawning biomass was estimated by the egg production method (EPM) (Lasker 1985). Beginning in 1986, the estimate was computed by the stock synthesis (SS) model (Methot 1986; Methot and Lo 1987). The SS model integrates the EPM observation with other data. These data include other biomass indexes, age composition from U.S. and Mexican fisheries, age composition from California Department of Fish and Game surveys, and environmental data. Although four time series of abundance data are used in the historical model, the new data points in 1988 are only (1) the modified historical egg production computed from plankton samples in the California Cooperative Oceanic Fisheries Investigation (CalCOFI) survey; (2) the 1987 age composition data from the Mexican fishery in Ensenada (pers. comm. Walterio Garcia Franco, Centro Regional Investigación de Pesquera [CRIP], Instituto Nacional de Pesca); and (3) the sea-surface temperature at the pier of the Scripps Institution of Oceanography.

MODEL

The SS model (figure 1) developed by Methot (1986) and revised by Methot and Lo (1987) and Methot (in press) used data on age composition and various biomass time series to construct time series of age-structured populations. The age-composition data provide information on recruitment variability and describe year-to-year changes in relative abundance; biomass time series establish the trend in abundance. The population from the model is characterized by a set of biological parameters, e.g., recruitment, natural mortality, age-specific availability to the fishery, and temperature-dependent fraction of age 1 anchovy that are mature. Other parameters are associated with fishery-independent biomass estimates. Parameter estimates are chosen so that the age compositions and biomass indexes

[Manuscript received February 2, 1989.]

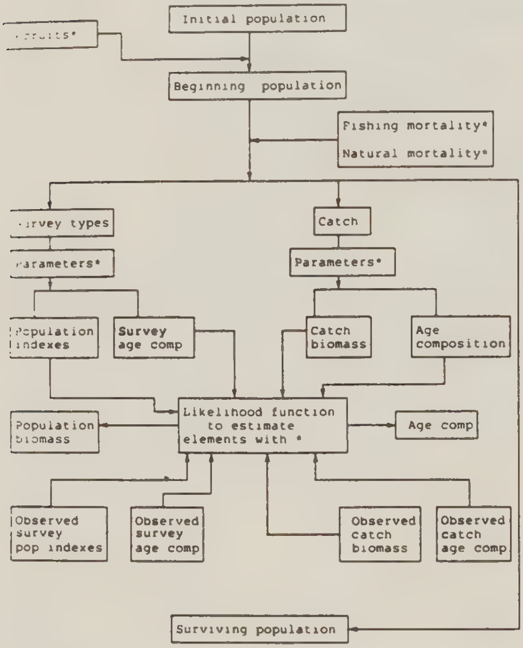


Figure 1. Schematic stock synthesis model. Asterisks indicate parameters to be estimated by the model.

computed from the model closely match the "observed" values. The best estimates are those that maximize a composite likelihood function. These estimates are then used in the population model to compute biomass at age and the spawning biomass (figure 1).

The observed age compositions are obtained from commercial catches of the U.S. and Mexican fisheries and from U.S. sea surveys. The observed biomass may be any existing biomass time series. The current SS model uses spawning biomass time series (table 1) from the egg production method (Lasker 1985; Bindman 1985), historical egg production (HEP) (Lo 1985), sonar (Mais 1974), and modified HEP (Methot and Lo 1987). The environmental variable, sea-surface temperature (George Anderson, SIO, pers. comm.), is included to model the availability to the fishery, the fraction of one-year-olds that are mature, and the fraction of one-year-olds that are actively spawning (Methot, in press). The natural mortality was fixed at the value 0.6, which is consistent with the literature (MacCall 1974) and earlier investigation with the SS model (Methot 1986).

TABLE 1
Fishery-Independent Spawning Biomass Estimate for Northern Anchovy

Year	EPM	HEP	MHEP	*Z*	Sonar
1951	–	0.012 (0.12)	0.011 (0.06)	0.23 (2.18)	–
1952	–	0.017 (0.11)	0.024 (0.14)	.09 (1.27)	–
1953	–	0.066 (0.18)	0.035 (0.08)	.19 (0.54)	–
1954	–	0.168 (0.19)	0.177 (0.18)	.12 (0.24)	–
1955	–	0.316 (0.34)	0.360 (0.41)	.07 (0.26)	–
1956	–	0.146 (0.65)	0.476 (2.21)	.33 (0.88)	–
1957	–	0.364 (0.42)	0.444 (0.47)	.20 (0.25)	–
1958	–	1.274 (1.18)	1.718 (1.23)	.43 (0.23)	–
1959	–	0.992 (0.82)	1.777 (1.31)	.23 (0.20)	–
1960	–	1.765 (0.77)	2.443 (1.20)	.24 (0.10)	–
1961	–	0.653 (0.64)	0.706 (0.61)	.29 (0.22)	–
1962	–	1.314 (1.17)	2.248 (1.66)	.19 (0.18)	–
1963	–	2.275 (0.99)	2.967 (1.39)	.28 (0.09)	–
1964	–	4.147 (2.68)	8.643 (4.59)	.42 (0.13)	–
1965	–	4.019 (1.18)	8.177 (2.91)	.19 (0.06)	–
1966	–	5.256 (1.80)	12.851 (5.12)	.42 (0.07)	–
1967	–	–	–	–	–
1968	–	–	–	–	–
1969	–	3.821 (1.06)	5.431 (1.55)	.19 (0.06)	438
1970	–	–	–	–	275
1971	–	–	–	–	233
1972	–	1.657 (0.80)	3.450 (0.83)	.25 (0.11)	822
1973	–	–	–	–	1671
1974	–	–	–	–	947
1975	–	19.691 (10.36)	16.707 (3.96)	.44 (0.11)	3086
1976	–	–	–	–	–
1977	–	–	–	–	1984
1978	–	2.33 (4.48)	14.657 (6.53)	.59 (0.10)	392
1979	–	5.426 (2.62)	5.070 (2.19)	.48 (0.10)	292
1980	870	2.671 (1.26)	2.548 (0.99)	.36 (0.08)	604
1981	635	4.376 (2.08)	4.738 (1.78)	.38 (0.08)	567
1982	415	3.29 (1.36)	1.684 (2.03)	.36 (0.09)	250
1983	652	3.91 (1.17)	1.654 (1.27)	.46 (0.06)	532
1984	309	2.85 (1.06)	2.567 (1.76)	.36 (0.08)	573
1985	521	2.62 (0.67)	5.160 (2.16)	.28 (0.05)	1015
1986	–	–	7.558 (3.34)	.34 (0.12)[a]	–
1987	–	–	7.234 (2.57)	.19 (0.08)[a]	–
1988	–	–	6.891 (3.42)	.53 (0.09)[a]	–

[a] *Z* for 1986–88 computed from the condensed CalCOFI area.

EPM is spawning biomass (thousand MT) estimated by the egg production method; HEP is the historical egg production index of spawning biomass (Lo 1985); MHEP is HEP as modified to account for the reduced CalCOFI sampling pattern. *Z* is the daily egg mortality associated with the HEP estimate and was used in making the MHEP estimate. Sonar is based on the acoustic surveys conducted by CDFG. Standard errors are in parentheses.

DATA

Fishery Data

The total landings from the U.S. fishery in 1987 were 5,024 MT, compared to 5,500 MT in 1986 (table 2). The total landings included 149 MT for reduction to oil and meal, and 4,875 MT for live bait and other uses (Thomson et al. 1988). The total landings at Ensenada, Baja California, Mexico, during 1987 were 124,457 MT (Secretaria de Pesca de México 1988; W. Garcia F., pers. comm.) compared to 96,000 MT in 1986. The 1987 landings are

TABLE 2
United States Fishery Landings and Weight at Age

Year	Month	Landings (MT)	Weight at age (g)					
			0	1	2	3	4	5+
1964	1–2	0						
	3–6	3482	0.0	12.9	17.5	21.0	24.5	28.8
	7–8							
	9–12	3484	11.2	16.6	19.4	21.8	24.4	26.3
1965	1–2							
	3–6	4122	0.0	12.9	17.5	21.0	24.5	28.8
	7–8							
	9–12	4124	11.2	16.6	19.4	21.8	24.4	26.3
1966	1–3	4518	2.7	12.1	15.8	19.4	23.4	28.5
	4–6	14440	6.7	13.6	17.4	20.1	22.9	28.0
	7–9	4958	10.8	15.1	18.4	20.0	22.3	26.9
	10–11	3851	12.3	17.1	19.4	21.7	23.9	26.3
1967	12–2	16982	1.8	11.4	16.6	19.5	22.4	26.0
	3–6	16934	5.9	11.7	17.7	22.3	28.1	33.3
	7–9	3876	10.9	15.2	18.4	19.9	22.3	26.8
	10–12	5307	12.1	16.9	19.5	21.8	24.1	26.8
1968	1–3	979	2.8	12.1	15.7	19.2	23.2	28.5
	4–6	3308	6.9	13.6	17.5	20.0	22.7	28.0
	7–9	4487	10.9	15.2	18.4	19.9	22.3	26.8
	10–1	13868	14.9	17.4	20.2	23.1	27.1	31.3
1969	2–3	2445	3.8	14.2	16.0	21.0	20.7	24.1
	4–5	10134	5.9	14.3	16.2	20.4	24.7	27.1
	6–8	4676	9.1	13.7	18.3	20.1	22.1	27.8
	9–12	47099	12.7	17.7	21.4	25.1	29.0	32.7
1970	1	6089	1.3	13.8	17.8	20.0	26.1	27.8
	2–5	23663	5.1	12.7	17.8	20.8	27.4	33.1
	6–10	30437	11.8	17.5	21.6	24.3	29.3	27.8
	11–12	32664	14.1	17.6	21.9	25.3	31.7	35.4
1971	1	9128	1.3	13.5	18.7	22.5	25.9	32.5
	2–5	10881	5.8	13.9	18.2	24.9	27.3	31.4
	6–9	7359	9.9	14.5	18.3	20.0	22.2	27.1
	10–12	19117	13.4	14.8	17.1	22.5	24.2	25.3
1972	1–2	11734	1.9	12.5	15.1	18.2	24.3	27.8
	3–5	16426	5.7	12.2	15.5	19.0	24.8	27.1
	6–9	9508	9.9	14.6	18.3	20.0	22.2	27.0
	10–12	30325	12.8	13.8	16.5	19.0	24.8	26.0
1973	1–2	3483	1.7	8.9	11.1	13.7	14.0	27.9
	3–6	36629	6.2	12.8	14.3	17.0	21.1	28.5
	7–10	38266	8.5	14.0	16.2	18.5	21.6	29.3
	11–12	47587	13.7	15.8	18.9	22.1	25.7	29.9
1974	1–2	11824	2.0	10.7	12.9	15.4	17.7	25.0
	3–6	18989	6.1	13.0	15.6	18.3	22.0	26.4
	7–9	5084	11.1	15.4	18.4	19.9	22.3	26.6
	10–1	61075	10.7	17.1	18.0	20.8	22.7	24.7
1975	2–3	13491	3.2	13.7	17.6	18.7	21.4	26.1
	4–6	34132	6.1	17.1	20.7	21.7	24.2	27.4
	7–10	42862	15.1	18.1	19.5	20.3	22.6	23.6
	11–1	60267	9.0	18.3	20.6	22.3	26.9	27.3
1976	2–3	12557	3.9	10.4	19.6	22.9	25.0	30.4
	4–6	19887	5.7	14.5	20.5	23.0	23.9	28.0
	7–9	10229	11.6	17.1	19.1	20.7	22.2	24.6
	10–1	61069	10.4	15.8	20.4	22.0	23.7	25.2
1977	2	503	2.7	11.7	15.2	17.4	21.1	27.7
	3–6	32294	4.7	13.9	15.5	19.1	22.5	26.5
	7–9	13483	12.8	18.0	19.3	21.0	22.4	25.7
	10–12	58869	12.2	18.4	20.3	22.1	22.9	26.2
1978	1–3	832	3.0	12.1	15.7	19.2	23.2	28.5
	4–6	3052	6.7	13.6	17.4	20.0	22.9	28.0
	7–9	6031	12.2	17.0	18.9	25.0	22.3	26.4
	10–12	7556	11.0	18.3	19.8	23.7	20.3	28.6
1979	1–3	625	2.6	12.0	15.7	19.1	23.1	28.4
	4–6	41754	6.5	14.3	18.6	22.5	24.8	24.9
	7–9	4563	11.3	15.6	18.4	19.9	22.3	26.4
	10–1	8591	8.8	19.2	23.0	20.0	24.9	26.6

(continued on next page)

TABLE 2 *(continued)*
United States Fishery Landings and Weight at Age

Year	Month	Landings (MT)	Weight at age (g) 0	1	2	3	4	5+
1980	2–3	207	3.5	12.2	15.7	19.1	23.1	28.6
	4–6	26730	6.8	11.2	18.4	20.8	24.1	27.7
	7–9	3374	11.0	15.2	18.4	19.9	22.3	26.8
	10–1	27401	9.5	14.2	19.2	21.5	22.8	27.6
1981	2–3	432	3.4	12.2	15.6	18.9	22.9	28.5
	4–6	34699	6.5	14.0	15.8	19.7	21.9	28.6
	7–9	2878	11.0	15.3	18.4	19.9	22.3	26.7
	10–1	9151	7.6	17.0	18.3	20.4	25.1	26.8
1982	2–3	375	3.4	12.2	15.6	19.0	23.0	28.6
	4–6	40808	7.3	14.4	18.5	20.2	22.2	25.2
	7–9	3044	10.6	14.8	18.4	20.0	22.3	27.2
	10–12	2872	11.9	16.8	19.4	21.5	23.7	26.5
1983	1–3	526	3.2	12.2	15.8	19.4	23.5	28.7
	4–6	4561	7.4	13.4	17.8	20.1	22.4	27.9
	7–9	2218	10.6	14.9	18.4	20.0	22.3	27.2
	10–12	1182	12.2	17.0	19.4	21.7	23.9	26.5
1984	1–3	427	2.5	11.9	15.7	19.0	22.9	28.3
	4–6	3680	6.8	13.6	17.4	20.0	22.8	28.0
	7–9	2266	10.5	14.9	18.4	20.0	22.3	27.2
	10–12	929	12.0	16.8	19.4	21.5	23.8	26.5
1985	1–3	503	2.8	12.0	15.6	18.8	22.7	28.3
	4–6	1064	7.3	13.5	17.7	20.1	22.5	28.0
	7–9	2727	10.7	15.0	18.4	20.0	22.3	27.1
	10–12	1490	12.1	16.9	19.5	21.7	24.0	26.7
1986	1–3	456	2.7	12.1	15.8	19.3	23.2	28.5
	4–6	1648	6.4	13.8	17.2	19.9	23.1	28.1
	7–9	2519	10.6	14.9	18.4	20.0	22.3	27.2
	10–12	881	12.1	16.9	19.4	21.6	23.9	26.6
1987	1–3	370	2.9	12.1	15.7	19.0	23.0	28.4
	4–6	1013	6.7	13.5	17.5	20.1	22.9	28.0
	7–10	2965	10.9	15.4	18.6	20.2	22.5	26.9
	11–12	527	12.4	17.1	19.6	22.2	24.5	26.8

62% of the 200,000-MT optimum yield. The landings data are necessary for calculating survivorship from the previous year's biomass estimate. Monthly landings, age composition, and weight-at-age data for 1987 were obtained from CRIP (tables 3–5. For data sources for years before 1987, see Methot 1986). The CRIP port sampling program collected monthly anchovy samples from randomly selected fishing boats. Hundreds to thousands of fish were measured, and age was determined from otolith readings (W. Garcia F., pers. comm.). The age composition from the autumn fishery reveals

TABLE 3
Mexican Fishery Data, 1987

Month	Landings (MT)	Age composition 0	1	2	3	4	5+	*N* aged	Weight at age (g) × 10 0	1	2	3	4	5+
1	73	0	0	0	0	0	0	0	0[a]	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	95	0	468	33	7	4	0	512	0	63	120	120	130	0
4	4359	0	684	241	60	12	8	1005	0	99	104	133	186	178
5	23041	0	1105	189	74	28	15	1411	0	104	106	174	199	218
6	16455	368	491	43	45	11	23	981	40	152	133	221	232	246
7	22298	512	476	122	39	3	4	1156	47	125	128	144	195	214
8	29768	338	201	251	14	2	0	806	71	135	130	155	223	0
9	16291	1359	180	668	91	3	0	2301	67	121	111	118	117	0
10	11030	493	33	332	187	36	8	1089	75	127	134	128	129	159
11	1065	253	44	82	12	0	0	391	90	109	127	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0

[a] In Weight at age section, 0 indicates that no samples were taken.

TABLE 4
Mexican Fishery Landings and Weight at Age

Year	Month	Landings (MT)	Weight at age (g) 0	1	2	3	4	5+
Yearly data								
1964	3	4599	8.5	12.5	14.4	16.0	17.6	18.6
1965	3	9171	8.5	12.5	14.4	16.0	17.6	18.6
1966	3	13243	8.5	12.5	14.4	16.0	17.6	18.6
1967	3	20104	8.5	12.5	14.4	16.0	17.6	18.6
1968	3	14267	8.5	12.5	14.4	16.0	17.6	18.6
1969	3	3871	8.5	12.5	14.4	16.0	17.6	18.6
1970	3	27977	8.5	12.5	14.4	16.0	17.6	18.6
1971	3	20079	8.5	12.5	14.4	16.0	17.6	18.6
1972	3	30047	8.5	12.5	14.4	16.0	17.6	18.6
1973	3	15424	8.5	12.5	14.4	16.0	17.6	18.6
Seasonal data								
1974	1–3	0						
	4–6	12552	0.0	9.5	11.2	13.4	15.0	16.5
	7–9	19115	8.5	12.5	14.4	16.0	17.6	18.6
	10–12	11143	8.2	12.8	14.6	18.1	19.2	18.6
1975	1–3	6897	1.5	8.7	13.2	15.9	17.0	20.8
	4–6	21191	7.0	10.8	13.9	15.5	16.8	20.8
	7–8	20733	6.3	11.8	14.7	15.6	17.4	20.8
	9–12	8056	6.0	11.3	14.1	15.2	17.9	20.8
1976	1–3	253	2.2	8.9	13.3	15.8	17.0	20.8
	4–5	2492	5.0	10.0	13.5	15.6	16.8	20.8
	6–9	36686	6.4	11.5	14.6	15.5	17.7	20.8
	10–1	38745	7.7	11.3	14.3	15.6	17.5	20.8
1977	2–3	2204	2.7	9.4	13.4	15.8	17.0	20.8
	4–5	9884	5.0	10.0	13.5	15.6	16.8	20.8
	6–8	90522	6.3	11.6	14.6	15.6	17.5	20.8
	9–1	37692	6.5	11.5	14.2	15.7	17.7	20.8
1978	2–3	0	0.0	0.0	0.0	0.0	0.0	0.0
	4–5	12089	5.2	10.0	13.5	15.5	16.7	20.8
	6–8	72637	9.2	13.6	15.4	17.3	18.8	20.8
	9–1	56261	10.4	14.6	16.3	19.2	18.0	20.8
1979	2–3	0	0.0	0.0	0.0	0.0	0.0	0.0
	4–6	78899	6.9	11.6	12.8	15.0	17.2	20.7
	7–8	45929	7.4	11.8	13.3	16.6	17.5	20.8
	9–1	81238	7.1	12.0	13.6	16.9	17.9	20.8
1980	2–3	139	2.8	9.4	13.4	15.8	17.0	20.8
	4–5	4611	5.4	10.2	13.9	15.7	17.0	20.8
	6–8	130810	7.7	12.9	16.1	17.0	18.7	20.8
	9–1	110940	8.5	13.0	16.0	17.7	18.8	20.8
1981	2–3	0	0.0	0.0	0.0	0.0	0.0	0.0
	4–6	71423	7.4	10.7	12.6	14.3	15.4	20.8
	7–9	144543	7.6	10.7	12.6	14.0	16.2	20.8
	10–1	39420	8.4	11.4	13.3	14.7	14.9	20.8
1982	2–3	0	0.0	0.0	0.0	0.0	0.0	0.0
	4–5	27240	5.3	12.4	14.3	15.9	16.5	21.5
	6–8	105296	8.2	12.1	13.5	14.8	15.3	23.4
	9–10	24695	7.3	11.9	13.5	14.7	15.4	22.5
1983	11–3	24418	1.1	6.7	9.0	10.1	12.1	18.6
	4–5	35725	5.3	7.1	8.7	9.1	17.6	21.0
	6–8	18308	6.7	8.7	10.2	11.0	17.8	23.8
	9–2	21341	3.3	7.1	8.0	9.7	13.9	22.5
1984	3–4	590	4.4	6.9	8.1	11.1	17.4	18.2
	5–6	36495	5.6	8.6	13.7	16.0	17.5	23.7
	7	25465	4.9	9.2	12.7	12.1	17.3	22.5
	8–1	38546	5.0	8.5	12.0	15.2	15.8	22.5
1985	2	0	0.0	0.0	0.0	0.0	0.0	0.0
	3–6	59348	5.1	14.1	15.7	18.3	18.7	20.6
	7	17894	6.4	18.8	20.1	26.2	25.0	22.5
	8–1	44547	7.1	18.5	20.9	22.3	22.6	22.5
1986	2–3	211	2.7	6.5	12.4	15.4	17.0	18.2
	4–5	7334	4.7	8.4	13.8	16.4	16.6	20.2
	6–7	36648	8.1	13.1	16.0	20.7	20.9	23.7
	8–12	51478	5.3	12.9	15.5	19.7	18.6	22.5

(continued on next page)

TABLE 4 *(continued)*

Mexican Fishery Landings and Weight at Age

Year	Month	Landings (MT)	Weight at age (g) 0	1	2	3	4	5+
1987	1–3	168	2.2	6.3	12.2	13.7	15.3	18.2
	4–5	27400	5.3	10.3	10.5	16.7	19.8	21.3
	6–7	38753	4.4	13.8	12.9	18.3	22.3	24.1
	8–12	58154	7.1	13.2	12.6	13.1	14.4	21.5

TABLE 5

Age Composition for U.S. Fishery, Mexican Fishery, and U.S. Survey

Year	Qtr.	Type	Age 0	1	2	3	4	5+	N aged
1967	1	US-F	0.0	39.0	224.3	662.3	704.0	239.0	1870
	2	US-F	0.0	42.3	167.0	265.6	165.7	96.4	739
1968	1	US-S	0.0	422.0	305.0	149.0	111.0	14.0	105
	2	US-S	0.0	144.0	248.0	189.0	259.0	161.0	245
	4	US-F	39.1	358.1	285.0	92.4	60.8	6.2	845
1969	1	US-F	0.0	62.7	73.7	26.0	6.6	10.1	179
	2	US-F	0.0	200.8	389.9	119.7	50.1	30.5	789
	4	US-F	101.2	722.6	1664.8	423.3	80.1	12.0	3003
1970	1	US-F	0.0	167.0	352.0	207.0	44.0	16.0	786
	1	US-S	0.0	359.0	322.0	250.0	47.0	22.0	206
	2	US-F	0.0	1191.0	528.9	338.3	73.7	18.1	2153
	3	US-F	4.5	411.3	902.0	302.9	34.3	3.0	1657
	4	US-F	42.0	682.0	756.0	480.0	57.0	9.0	2024
1971	1	US-F	0.0	69.0	367.0	304.0	243.0	67.0	1050
	1	US-S	0.0	196.0	301.0	307.0	164.0	33.0	173
	2	US-F	0.0	54.4	89.6	95.8	51.7	20.5	312
	2	US-S	0.0	223.0	281.0	300.0	132.0	64.0	171
	4	US-F	62.5	477.2	365.7	94.5	24.1	0.7	1029
1972	1	US-F	0.0	106.8	890.9	366.4	147.7	44.0	1557
	2	US-F	0.0	154.5	424.9	192.8	79.1	15.6	867
	2	US-S	0.0	122.0	412.0	253.0	119.0	94.0	190
	4	US-F	74.1	500.2	1561.2	431.6	37.8	9.1	2616
1973	1	US-S	0.0	43.0	377.0	457.0	112.0	11.0	249
	2	US-F	0.0	425.9	864.5	1237.8	455.6	134.1	3116
	2	US-S	0.0	35.0	219.0	406.0	255.0	86.0	190
	3	US-F	6.0	319.3	985.6	907.5	153.8	10.8	2383
	4	US-F	27.6	269.5	935.9	1027.4	264.5	24.0	2548
1974	1	US-F	0.0	263.9	607.5	471.9	260.1	37.8	1640
	2	US-F	0.0	157.0	274.7	174.2	134.0	42.1	782
	2	US-S	0.0	28.0	144.0	333.0	396.0	100.0	290
	4	US-F	43.2	579.7	1694.7	966.9	301.0	18.9	3611
1975	1	US-F	0.0	154.9	231.0	252.1	170.2	83.8	892
	1	MX-F	0.0	49.8	65.2	186.6	60.7	9.7	372
	1	US-S	0.0	84.0	153.0	273.0	262.0	228.0	220
	2	US-F	0.0	52.9	317.3	656.8	598.6	343.5	1970
	2	MX-F	1.3	8.0	77.2	144.4	49.5	7.7	288
	3	US-F	13.0	369.7	1187.9	738.5	162.9	27.2	2498
	3	MX-F	4.3	16.5	70.9	114.0	37.5	5.7	249
	4	US-F	59.9	297.0	1345.2	1342.5	531.7	46.5	3625
	4	MX-F	21.5	24.5	37.0	62.0	25.2	5.8	176
1976	1	US-F	0.0	52.1	57.7	180.1	263.0	257.7	809
	2	US-F	0.0	7.0	89.1	299.9	467.2	286.8	1151
	2	MX-F	0.0	27.4	100.3	189.1	66.7	8.5	392
	2	US-S	0.0	16.0	24.0	151.0	430.0	380.0	320
	3	US-F	0.0	36.0	67.0	76.0	13.0	1.0	193
	3	MX-F	170.3	144.2	151.1	175.1	78.5	10.7	730
	4	US-F	306.2	255.2	579.8	1086.1	535.3	93.3	2856
	4	MX-F	376.2	59.9	81.5	36.8	10.6	0.0	565

(continued on next page)

TABLE 5 *(continued)*
Age Composition for U.S. Fishery, Mexican Fishery, and U.S. Survey

Year	Qtr.	Type	Age						*N* aged
			0	1	2	3	4	5+	
1977	1	MX-F	0.0	93.0	39.5	113.2	51.3	0.0	297
	1	US-S	0.0	450.0	47.0	96.0	216.0	191.0	470
	2	US-F	0.0	908.7	250.2	187.8	264.1	212.2	1823
	2	MX-F	0.0	98.4	47.3	66.1	55.4	24.8	292
	3	US-F	5.0	158.0	76.0	40.0	50.0	10.0	339
	3	MX-F	34.1	215.2	166.3	233.0	182.1	40.2	871
	4	US-F	262.9	886.3	506.8	379.6	358.3	77.0	2471
	4	MX-F	115.2	183.1	115.4	112.2	51.9	15.2	593
1978	1	US-S	0.0	96.0	459.0	160.0	149.0	135.0	396
	3	MX-F	146.5	151.4	1043.1	62.8	39.0	23.2	1466
	4	US-F	71.4	107.3	114.5	4.9	7.3	1.7	307
	4	MX-F	1353.8	170.6	303.6	9.4	8.1	3.5	1849
1979	1	US-S	0.0	652.0	95.0	180.0	64.0	8.0	508
	2	US-F	0.0	2453.2	720.9	432.7	63.8	18.5	3688
	2	MX-F	6.9	1096.8	430.2	146.3	7.0	1.9	1689
	2	US-S	0.0	727.0	132.0	97.0	25.0	18.0	328
	3	MX-F	48.1	799.9	155.1	49.6	2.2	0.0	1055
	4	MX-F	744.1	1112.4	135.7	45.1	1.6	0.0	2039
1980	1	US-S	0.0	348.0	501.0	120.0	22.0	8.0	610
	2	US-F	0.0	915.6	1170.1	159.6	23.2	2.4	2270
	2	MX-F	0.0	241.0	202.7	21.5	14.8	0.0	480
	3	MX-F	15.9	763.2	1089.2	107.3	20.5	0.0	1996
	4	US-F	135.2	1008.6	736.6	77.6	10.0	0.0	1966
	4	MX-F	750.5	723.5	607.9	57.5	3.7	0.0	2143
1981	1	US-S	0.0	453.0	305.0	205.0	34.0	2.0	555
	2	US-F	0.0	1177.1	902.8	583.3	59.4	2.0	2724
	2	MX-F	12.0	1490.3	789.6	282.1	24.1	0.0	2598
	2	US-S	0.0	297.0	316.0	379.0	8.0	0.0	460
	3	MX-F	130.8	1246.4	583.0	215.2	21.6	0.0	2197
	4	US-F	8.3	125.5	168.8	29.4	0.0	0.0	332
	4	MX-F	441.2	737.6	411.7	148.4	14.6	3.5	1757
1982	1	US-S	0.0	93.0	360.0	477.0	68.0	0.0	651
	2	US-F	0.0	389.7	849.9	1137.8	293.2	2.9	2672
	2	MX-F	0.0	70.1	367.4	154.2	45.0	0.2	637
	3	MX-F	57.1	374.5	641.5	179.7	26.3	0.0	1279
	4	MX-F	317.3	146.9	164.2	29.6	1.9	0.0	660
1983	1	MX-F	0.0	399.1	223.1	54.8	3.1	0.0	680
	1	US-S	0.0	742.0	112.0	108.0	38.0	0.0	582
	2	MX-F	0.0	431.6	41.3	7.1	0.0	0.0	480
	3	MX-F	56.4	431.4	44.2	8.1	0.0	0.0	540
	4	MX-F	393.2	369.7	49.1	7.9	0.0	0.0	820
1984	1	US-S	0.0	348.0	585.0	53.0	13.0	0.0	518
	2	MX-F	30.7	510.1	269.5	23.0	5.7	0.0	839
	3	MX-F	93.0	217.0	29.0	1.0	0.0	0.0	340
	4	MX-F	1298.9	449.2	31.9	0.0	0.0	0.0	1780
1985	1	US-S	0.0	718.0	191.0	76.0	5.0	8.0	464
	2	MX-F	0.0	644.4	571.5	176.4	13.6	4.0	1410
	4	MX-F	755.6	168.1	113.0	32.9	6.4	0.0	1076
1986	1	US-S	0.0	170.0	598.0	203.0	24.0	5.0	790
	2	MX-F	0.0	476.9	130.0	57.2	13.2	2.6	680
	3	MX-F	90.5	828.6	67.3	9.3	3.2	1.1	1000
	4	MX-F	779.2	292.7	58.6	21.6	8.0	0.0	1160
1987	1	MX-F	0.0	468.0	33.0	7.0	4.0	0.0	512
	2	MX-F	0.0	1852.6	364.3	129.5	44.9	24.7	2416
	3	MX-F	885.0	960.5	169.5	83.1	13.4	25.5	2137
	4	MX-F	2191.8	721.9	1387.1	243.6	36.3	6.4	4587

Fishery age composition is in numbers of fish at age. Fractional fish are due to the weighting of raw monthly age compositions by the monthly landings. Survey age composition is expressed in thousandths and should be scaled by *N* aged.

the level of recruitment and number of age 0 fish. A temperature-dependent fraction of these recruits contributes to the coming winter's spawning biomass (Methot, in press).

Four periods were defined in each year, based on distinct changes in monthly landings, age composition, and weight at age (Methot and Lo 1987) (tables 2–5). Within each period, monthly age composition and weight-at-age data were weighted by the total landings for that month before combining with other months in the period. The U.S. nonreduction fishery landings were similar to 1986, and weights at age were assumed to be equal to the historical mean (table 2) (Methot and Lo 1987). The four periods of the 1987 Mexican fishery are similar to 1986 except for month 4–5, when 1987 landings are higher than for the same period of 1986 (tables 3 and 4). The weight at age in the fourth period is significantly smaller than the long-term average for fish of age >2 (table 4). In particular, the mean weight of four-year-old anchovy was only 14.4 g, whereas the average from 1974–86 was 17.9 (SD = 1.96); these fish were born in the El Niño year of 1983. The fraction of age 0 fish in the Mexican fishery in the last period in 1987 was 0.48 as compared to 0.67 in 1986 (table 5).

Modified Historical Egg Production Index

Spawning biomass of northern anchovy is measured most accurately by the egg production method (EPM), which was used during the period 1980–85. This method measures the abundance of newly spawned eggs and the rate at which mature adults are producing eggs. Estimates of the abundance of newly spawned eggs before 1980 were made by Lo (1985), using data from CalCOFI surveys. This index of historic egg production (HEP) included samples from approximately San Francisco, California, to Punta Baja, Baja California (30°N) during January–April (figure 2). The egg production values and mortality rate were estimated by the solutions to two equations: the abundance of eggs as the integral of mortality curve, and newly hatched larvae as the eggs at hatching time.

Beginning in 1985 the CalCOFI survey pattern changed. The frequency of surveys was increased from almost monthly every three years to quarterly each year, and the geographic extent was restricted to CalCOFI lines 77.0 (rounding off from 76.7, Pt. Buchon, California, north of Pt. Conception) to 93.0 (rounding off from 93.3, Del Mar, California, north of San Diego; figure 2). This change required a recalibration of the HEP index because the mean egg density in this restricted area is not expected to be the same as the mean density in the larger area. Since 1980, only samples collected during February–March have been used for this revised index, because this is the period during which subsequent data are expected to be collected.

The modified historical egg production (MHEP) index was derived from the egg mortality curve: $P_t = P_0 \exp(-zt)$, where P_t is the abundance of some life stage (or size category) corrected for the duration of that stage, and z is the mortality rate. By rearranging the terms in the equation, one obtains $P_0 = P_t \exp(zt)$, and an estimate of P_0 can be computed if the egg mortality rate (z) and at least one age-specific egg production are known. Because of the reduced sample size in the modified survey area, estimates of z were taken from Lo (1985) for years before 1986, and were computed from staged eggs sampled from the current CalCOFI survey area for years after 1985 (table 1). P_t's can be computed from egg and larval data from the modified survey area. We have for the historical data set two P_t's that are reasonably close in age to the age at spawning; one for the egg stage (P_{egg}) and the other for the yolk-sac larvae (P_{ys}). The historical anchovy data base provides only the standing stock of anchovy eggs, with no information on the distribution of egg stages. To obtain an average egg production rate, we divided the standing stock by the average temperature-specific incubation time to obtain the egg production rate (P_{egg}) at the mid-age (t_{egg} = incubation time /2). From the morality curve fit to sized larvae (Lo 1985), we estimated the larval production rate at the age of yolk absorption (P_{ys}). Assuming that eggs and yolk-sac larvae suffer the same mortality, two initial egg production estimates were computed as follows:

$$P_{0\text{-}egg} = P_{egg} \exp(zt_{egg})$$
and
$$P_{0\text{-}ys} = P_{ys} \exp(zt_{ys}).$$

The MHEP egg production index is the average of the above two estimates:

$$\text{MHEP} = (P_{0\text{-}egg} + P_{0\text{-}ys})/2$$

The variance of MHEP was computed as

$$\text{var (MHEP)} = [\text{var}\,(P_{0\text{-}egg}) + \text{var}\,(P_{0\text{-}ys})]/4.$$

To compute the MHEP index for 1988, we used a total of 58 plankton samples on the Jan. 19–Feb 2, 1988, CalCOFI cruise (Methot and Lo 1987). Anchovy eggs were collected with the CalCOFI vertical egg tow (CalVET) plankton net (Smith et al. 1985). The mouth area of the net is 0.05 m². The mesh size of 0.15 mm is the maximum size to retain all anchovy eggs. The standard net tow is a vertical cast to 70 m in 1 minute, held at depth for 10 seconds, and retrieved in 1 minute. The larval data were obtained from bongo oblique net tows (figure 2). In the past 30 years, different gears were used to

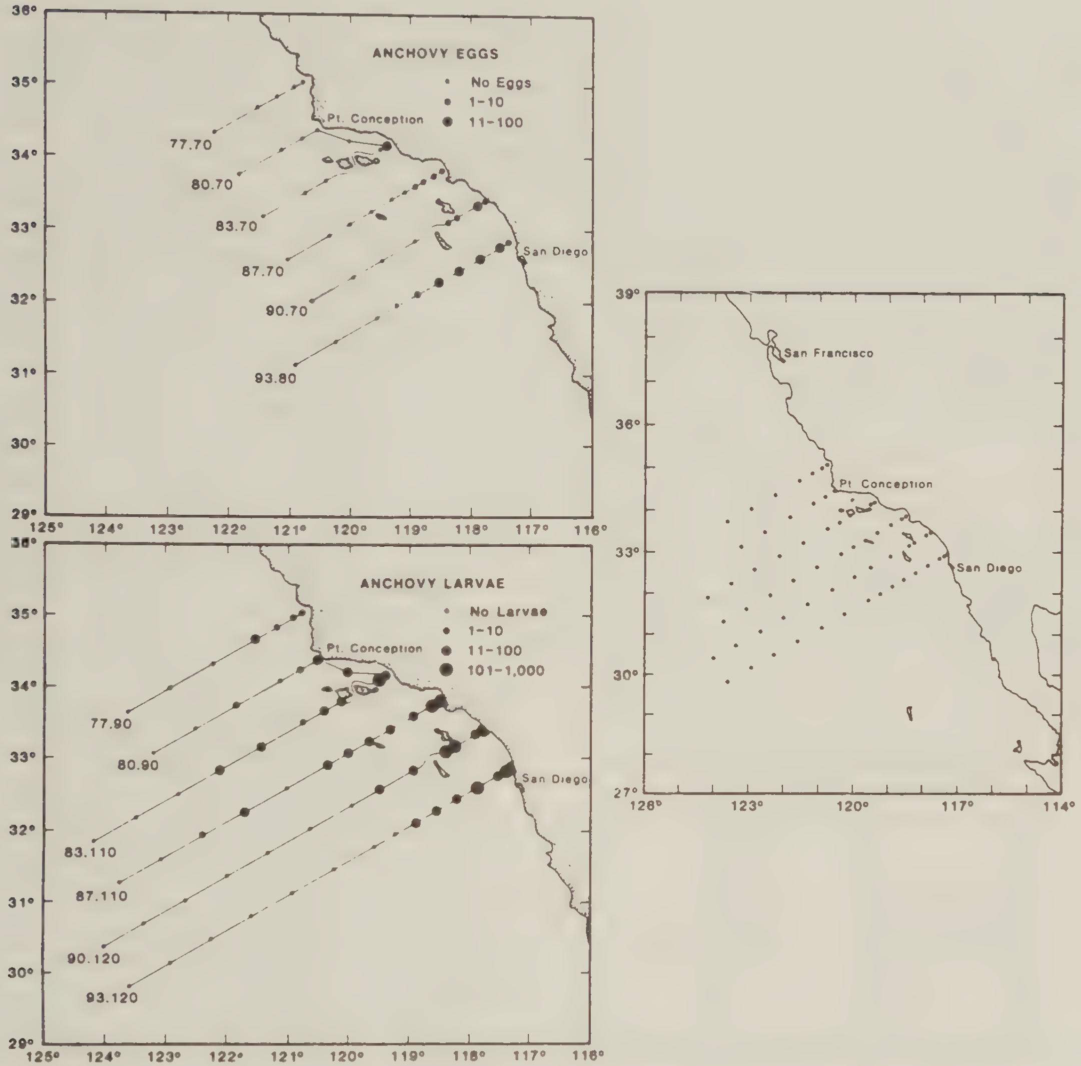


Figure 2. The map on the right shows the CalCOFI survey pattern since 1985 from Point Buchon, north of Point Conception, to Del Mar, north of San Diego, compared to the historical survey area from San Francisco to Punta Baja, Baja California. The maps on the left show the distribution of anchovy eggs and larvae from the 1988 CalCOFI survey. The number at the end of each line is the line and station number. The egg samples cover stations up to 70, except line 93

collect anchovy eggs and larvae for CalCOFI surveys. Calibration factors were used to standardize egg and larval catch (Lo 1985).

As mentioned earlier, the MHEP takes the average of two daily egg production rates, one based on eggs and the other on yolk-sac larvae. Both egg production rates incorporate the daily egg mortality (z), which was computed from staged eggs (table 1). Analysis of the number of eggs and yolk-sac larvae taken during the 1988 CalCOFI cruise indicated a daily egg mortality of -0.53 per day in 1988.

The estimated egg production rate for 1988 was $6.9/0.05\ m^2$/day (SE = 3.42), similar to 7.2 (SE = 2.57) in 1986 and 7.6 (SE = 3.34) in 1987. The biomass in 1988 appears to be higher than it was during the 1980–85 period, because in 1980–85 the average

TABLE 6

Time Series of Environmental Deviations and Weight-at-Age Deviations

Year	Qtr.	Temp.	WTDEV-US	WTDEV-MX
1964	2	.900		
	5	−.935		
	8	−.402		
	11	−.797		
1965	2	−1.122		
	5	.295		
	8	−1.351		
	11	.020		
1966	2	−.074		
	5	.274		
	8	.532		
	11	−.065		
1967	2	−.178	0.34	
	5	−.680	0.56	
	8	.021	—	
	11	1.050	—	
1968	2	−.005	—	
	5	.142	—	
	8	−.007	—	
	11	−.040	0.79	
1969	2	−.141	1.01	
	5	−.547	−0.29	
	8	−.563	—	
	11	−.283	1.99	
1970	2	−.124	1.68	
	5	.059	0.18	
	8	−.403	2.37	
	11	−.107	1.95	
1971	2	−.819	2.95	
	5	−1.580	1.38	
	8	.958	—	
	11	−1.022	−1.23	
1972	2	−1.716	−0.25	
	5	−.164	−1.31	
	8	.451	—	
	11	.156	−2.90	
1973	2	1.051	−4.67	
	5	−.354	−2.62	
	8	−.489	−2.37	
	11	−1.285	−0.45	
1974	2	−1.114	−2.30	
	5	−.494	−1.20	
	8	−.425	—	
	11	.185	−1.06	
1975	2	−1.041	1.34	
	5	−1.668	2.40	
	8	−1.481	0.47	
	11	−1.494	0.69	
1976	2	−.646	2.12	
1976	5	−.412	2.77	
	8	−.259	0.69	
	11	1.539	0.03	
1977	2	2.144	—	
	5	−.282	0.28	
	8	−.508	1.17	
	11	.474	1.12	
1978	2	1.562	—	
	5	1.181	—	
	8	−.422	0.91	1.13
	11	.783	0.85	2.48
1979	2	−.546	—	—
	5	−.301	0.95	0.44
	8	.157	—	0.33
	11	.086	2.01	−0.11
1980	2	.524	—	—
	5	.296	−0.18	0.37
	8	−.999	—	0.70
	11	−.883	−1.26	1.26
1981	2	.242	—	—
	5	1.061	−0.44	−0.43
	8	1.472	—	−1.03
	11	.073	−0.74	0.19
1982	2	−.093	—	—
	5	.282	0.51	1.30
	8	−.131	—	−0.20
	11	.559	—	0.53
1983	2	1.393	—	−2.29
	5	.808	—	−3.07
	8	.200	—	−2.91
	11	1.965	—	−3.90
1984	2	.924	—	−2.99
	5	1.091	—	−1.72
	8	2.184	—	−1.92
	11	2.000	—	−2.22
1985	2	−.427	—	—
	5	.015	—	2.94
	8	.614	—	4.59
	11	.953	—	1.63
1986	2	.602	—	—
	5	1.258	—	−1.07
	8	.130	—	1.44
	11	.734	—	−0.45
1987	2	1.230	—	0.00
	5	1.355	—	−0.34
	8	−.718	—	0.48
	11	1.566	—	−0.01
1988	2	−.083	—	—
	5	1.198	—	—

Deviations are calculated from monthly means, then averaged into quarters. Environmental deviations are lagged − 1 month (e.g., quarter 1 contains average Dec.–Feb. deviation). Temp. is the surface temperature at the SIO pier. WTDEV-US and WTDEV-MX are average weight-at-age deviations for ages 2–4 based on data from the commercial reduction fishery at San Pedro in the United States and ages 1–3 at Ensenada in Mexico.

daily egg production rate was only 3.1 if one assumes that the adult reproductive output in 1988 is similar to the average of 1980–85 (table 1).

Environmental Data

Temperature anomalies at the SIO pier were used as an indicator of environmental changes (table 6). During Jan.–Feb. 1988, the mean temperature at the SIO pier was 13.9°C, whereas it was 15°C in 1987 and 15.2°C in 1986 (figure 3). Monthly temperature deviations were averaged into trimonthly periods to be compatible with age-composition data. Two series of temperature indexes were derived from these temperature anomalies. The first series comprised short-term temperature indexes, which averaged the current and previous anomaly, with the

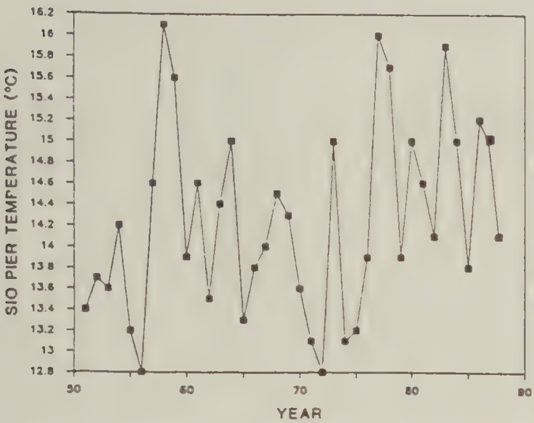


Figure 3. Time series of Jan.–Feb. water temperature (°C) at SIO, 1951–88

current anomaly having twice the weight of the previous. The second series comprised long-term temperature indexes, which used the current and 15 previous quarters with a linear weighting scheme, with the current value having a weight of 16. The first, high-frequency series was detrended by subtracting the second series from it.

The 1987 SS model also includes time series of weight-at-age deviations, which are used to model the availability to the fishery. Methot and Lo (1987) note that the fraction of age 3+ fish in the Mexican fishery was never greater than 0.02 when the weight of the age 2 fish was less than 12 grams. Appearance of small fish is an indication that the stock has shifted northward, thus a clue that availability to the geographically fixed fisheries should be modified. The weight-at-age deviations for the United States were reproduced from Methot and Lo (1987). The weight-at-age deviations for the Mexican fishery were recomputed by adding 1987 weight at age to the data set (table 6). Availability parameters were modeled as linear functions of environmental and weight deviations.

Methot (1986, in press) presents a relation between percentage of mature fish and temperature at the SIO pier. In 1988, at 13.9°C, the temperature-maturity relation indicates that 63% of the age 1 fish are sexually mature, and 33% of them are actively spawning according to the relationships:

$$\text{Fraction mature at age 1} = \exp(-33.4 + 2.44\ \text{temp})/[1 + \exp(-33.4 + 2.44\ \text{temp})]$$

and hence contribute to spawning biomass.

$$\text{Fraction of age 1 spawning} = \exp(-17.51 + 1.21\ \text{temp})/[1 + \exp(-17.51 + 1.21\ \text{temp})]$$

and hence contribute to the MHEP index.

One of the major sources of natural mortality of northern anchovy is believed to be predation by Pacific mackerel (Methot 1986). Pacific mackerel biomass was estimated to be 500,000 MT on July 1, 1987 (Methot and Lo 1987), and projected to be 290,000 MT on July 1, 1988 (Patty Wolf, CDFG, pers. comm.). The decrease of biomass was possibly due to the changed estimation procedure. (The historical time series of Pacific mackerel biomass are being reexamined; the results are not available at the time of this writing.) At the level of 290,000 MT of mackerel biomass, the model specifies that natural mortality of anchovy increases from the nominal level of 0.6 to a level of 0.7 per year.

RESULTS AND DISCUSSION

The spawning biomass in February 1988 is estimated to be 1,009,000 MT (table 7, figure 4). Although this value is a slight decrease from 1,212,000 MT in 1987 (Methot and Lo 1987), it is still higher than the 1985 spawning biomass of 521,000 MT, estimated by the EPM. The high level of spawning

TABLE 7
Time Series of Estimated Biomass and Recruitment

Year	Total biomass	Spawning biomass	Recruitment
1964	782	773	0.46
1965	705	607	0.20
1966	537	511	0.15
1967	369	354	0.52
1968	353	334	0.48
1969	374	348	0.55
1970	391	301	1.72
1971	723	309	1.63
1972	1040	605	2.35
1973	1440	1412	2.37
1974	1720	1148	0.80
1975	1432	1251	0.32
1976	1011	970	1.12
1977	826	825	0.25
1978	443	442	2.12
1979	813	536	1.72
1980	763	756	1.52
1981	806	768	0.57
1982	470	428	1.70
1983	556	538	0.71
1984	382	376	1.53
1985	675	529	1.01
1986	636	630	2.27
1987	900	878	3.00
1988	1297	1009	0.62

Biomass estimates are in units of thousand metric tons as of Feb. 15 of the indicated year. Recruitment estimates are in units of 50 billion age 0 fish as of July 1 of the indicated year.

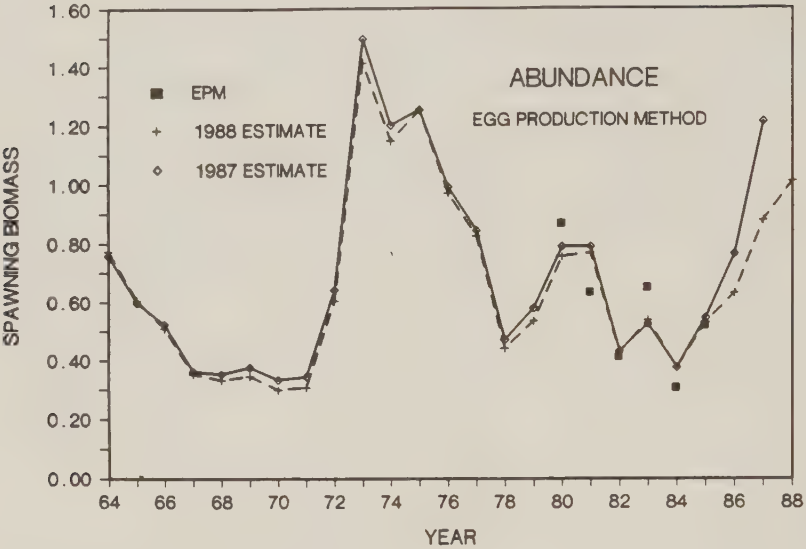


Figure 4. Estimated time series of spawning biomass, using data up to 1987, data up to 1988, and observations made by the egg production method.

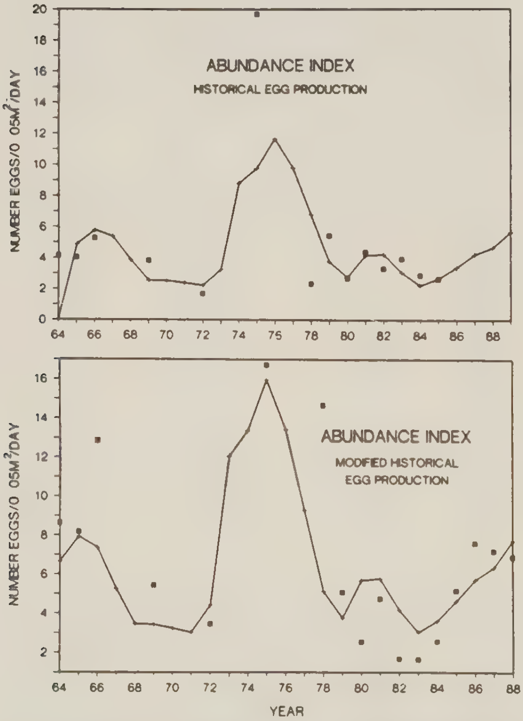


Figure 5. Estimated (squares) and observed (+) time series of historical egg production (Lo 1985) and modified HEP for the current CalCOFI survey area (see figure 2).

biomass was partially due to the high egg production rate estimated from MHEP (figure 5) and partially due to the strong incoming year class in 1987 (figure 6).

The SS model provided a time series of yearly biomass estimates (table 7). The computation of sample variance of the estimates, although it is technically feasible, has not been implemented in the model. Without variance estimates, it is impossible to judge the precision of the biomass estimate for a single year. However, a time series of biomass can indicate long-term change in the population, and it is useful for management.

The current estimate of the 1987 spawning biomass from the SS model using the 1964–88 time series is 880,000 MT; when the 1964–87 time series was used it was 1,212,000 MT (Methot and Lo 1987) (figure 4). Thus some uncertainties exist in estimating the magnitude of the 1986 and 1987 year classes. These year classes seem to be very abundant, because they dominate in the fourth-period Mexican fishery, even though their predicted availability to the fishery is one-third that of the 1984 and 1985 year classes (table 8). It is not surprising that the abundance of the second-year cohort differs from that of the first year, since the cohort in the second year is estimated from an additional year of age-composition data. For this reason, the first year's estimate of cohort biomass in the SS model will always be more uncertain than the subsequent year's estimate.

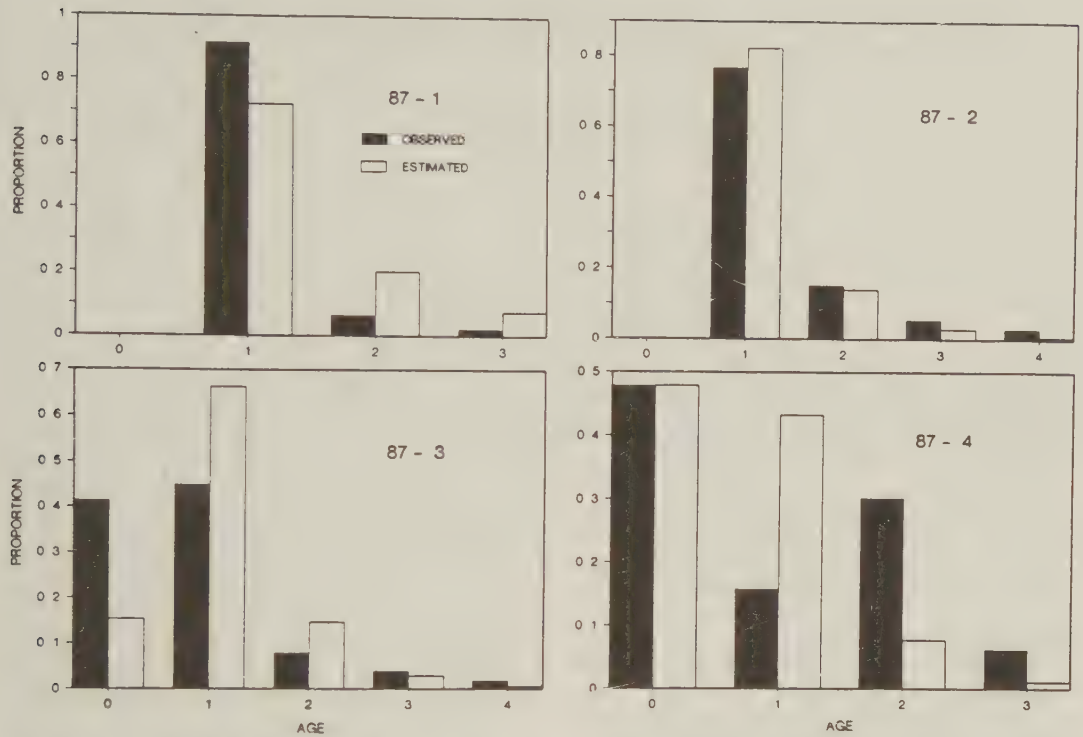


Figure 6. Observed and estimated age composition in 1987 for four periods: period 1, Jan.–Mar.; period 2, April and May; period 3, June and July; period 4, Aug.–Dec. (see table 3).

In the assessment conducted last year with data through the winter of 1987 (Methot and Lo 1987) the 1986 year class was fixed at a high value because when unconstrained, the model assigned an even higher value to the 1986 year class. The same situation occurred in the current assessment, which used data through winter 1988. In this case we fixed the abundance of the 1987 year class at a high value, and estimated the 1986 year class to be somewhat lower than the assumed large 1987 year class. Consequently, the revised estimate of the spawning biomass in 1987 declined when the additional year of data was included. This revised estimate of the 1987 spawning biomass, 880,000 MT, is nearly identical to the alternative estimate, 840,000 MT, made by Methot and Lo (1987) under the assumption that availability to the fourth-period Mexican fishery has been 1.0 since 1983.

The abundance of age 0 fish is difficult to assess because it is affected by two factors: the absolute abundance of age 0 fish in the population and the availability of these fish to the Mexican fishery. The availability of juvenile anchovy to the Mexican fishery is a critical parameter in the SS model. The abundance of juveniles relative to older fish in this fishery fluctuates because of year-to-year changes in the true relative abundance of these new recruits, and because of changes in their availability to the fishery. In the model, temporal changes in age-specific availability were assumed to be a function of long-term temperature trends, deviations from this trend, and deviation in weight at age. Estimated availability of these young fish to the Mexican fishery was very high during, and immediately following, the 1982–83 El Niño (table 8). Consequently, high incidence of young fish during this period is partially explained by their increased availability to the fishery. In the fourth periods of 1985, 1986, and perhaps 1987, the model predicts somewhat lower availability, while the abundance of age 0 fish stayed high. Thus the model indicates that the recruits of these three year classes were very abundant. We

TABLE 8

Recruitment to the Fishery at Ensenada, Mexico

	Age 0						Age 1					
	Period 3			Period 4			Period 1			Period 2		
Year class	O	E	AV	O	E	Av	O	E	Av	O	E	Av
1975	.017	.011	.004	.122	.026	.032	—	—	—	.070	.256	1.00
1976	.233	.091	.053	.666	.451	.468	.313	.576	.633	.337	.368	.211
1977	.039	.041	.007	.194	.198	.205	—	—	—	—	—	—
1978	.100	.152	.017	.732	.690	.194	—	—	—	.652	.692	.235
1979	.046	.146	.013	.365	.420	.162	—	—	—	.502	.447	.269
1980	.008	.065	.008	.350	.204	.048	—	—	—	576	.488	.349
1981	.060	.103	.039	.251	.231	.160	—	—	—	.110	.338	.260
1982	.045	.159	.015	.481	.632	.215	.587	.767	.384	.899	.873	1.00
1983	.104	.111	.015	.480	.362	.376	—	—	—	.631	.656	1.00
1984	.274	.213	.043	.730	.755	.714	—	—	—	.457	.592	.326
1985	—	—	—	.702	.530	.725	—	—	—	.701	.708	1.00
1986	.091	.171	.028	.672	.544	.230	.914	.722	.549	.767	.824	1.00
1987	.414	.153	.027	.478	.473	.234						

Note: Age 0 anchovy are partially recruited to this fishery in the third period of the year. They typically are fully recruited in the second period of the following year. The symbols indicate the observed ratio of recruits to total numbers in the Mexican fishery (O), the ratio expected by the model (E), and the estimated, environmentally sensitive availability used by the model (Av).

intend to reexamine the submodel that predicts availability from environmental deviations, but it seems unlikely that the generally good fit apparent in table 8 can be substantially improved.

ACKNOWLEDGMENTS

We thank all those who contributed to the spawning biomass estimate, in particular W. Garcia F. of CRIP, INP, Mexico, for providing the age-composition data of the Mexican fishery at Ensenada through the MEXUS-PACIFICO program; the individuals who collected, sorted, staged, and processed the plankton samples from the January 1988 CalCOFI cruise; all crew members of the NOAA ship *David Starr Jordan*; John Hunter for reading the manuscript; and two reviewers for their critiques.

LITERATURE CITED

Bindman, A. G. 1985. The 1985 spawning biomass of the northern anchovy. NMFS SWFC Admin. Rept. LJ-85-21, 21 pp.

Lasker, R., ed. 1985. An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy (*Engraulis mordax*). U.S. Dep. Commer. NOAA Tech. Rep. NMFS 36, 99 pp.

Lo, N. C. H. 1985. Egg production of the central stock of northern anchovy, *Engraulis mordax*, 1951–82. Fish. Bull., U.S. 83:137–150.

MacCall, A. D. 1974. The mortality rate of *Engraulis mordax* in southern California. Calif. Coop. Oceanic Fish. Invest. Rep. 17:131–135.

Mais, K. F. 1974. Pelagic fish surveys in the California Current. Calif. Dep. Fish Game Fish. Bull. 162, 79 pp.

Methot, R. D. 1986. Synthetic estimates of historical abundance and mortality for northern anchovy, *Engraulis mordax*. NMFS SWFC Admin. Rep. LJ-86-29, 85 pp.

———. In press. Synthetic estimates of historical abundance and mortality for northern anchovy. *In* Mathematical analysis of fish stock dynamics, E. Vetter and B. Megrey, eds.

Methot, R. D., and N. C. H. Lo. 1987. Spawning biomass of the northern anchovy in 1987. NMFS SWFC Admin. Rep. LJ-87-14, 46 pp.

PFMC. Pacific Fishery Management Council. 1983. Northern anchovy fishery management plan. PFMC, Metro Center, 2000 SW First Ave., Portland, OR 97201.

Secretaria de pesca de Mexico. 1988. Boletín anual temporada 1987, centro regional de investigación pesquera, ediado en coordinación con la cámara nacional de la industria pesquera delegación, Ensenada, Baja California.

Smith, P. E., W. Flerx, and R. P. Hewitt. 1985. The CalCOFI vertical egg tow (CalVET) net. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, R. Lasker, ed. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36, pp. 27–32.

Thomson, C., C. Scannell, and J. Morgan. 1988. Status for the California coastal pelagic fisheries in 1987. NMFS/SWFC Admin. Rep. LJ-88-18.

8940

AGAINST MARINE FISH HATCHERIES: IRONIES OF FISHERY POLITICS IN THE TECHNOLOGICAL ERA

ALEC D. MACCALL
Southwest Fisheries Center
3150 Paradise Drive
Tiburon, California 94920

ABSTRACT

Marine fish hatcheries have a long history of expensive operation with no demonstrable positive effect on the resource. It is exceedingly difficult to detect hatchery-produced fish. Although very expensive, full hatchery operation may be necessary to determine effectiveness. Modern techniques of genetic marking and fingerprinting provide new tools for determining hatchery success. Unfortunately, legislation to fund research on hatcheries is forestalling vitally needed legislation to stop further deterioration of fish stocks. Popular interest in marine fish hatcheries is having a deleterious rather than beneficial effect on the resources.

RESUMEN

Las piscifactorías marinas poseen una larga historia de costosas operaciones que no han demonstrado un efecto positivo sobre el recurso pesquero. Resulta excesivamente dificultoso detectar peces de criaderos. A pesar del alto costo, tal vez sea necesario mantener criaderos totalmente funcionales por un tiempo prolongado para determinar su eficacia. Las técnicas modernas de marcación genética e identificación individual (equivalente al uso de impresiones digitales) proveen nuevas herramientas para determinar el éxito de un determinado criadero. Nos urge la necesidad de una legislación que legisle la disponibilidad de fondos para la investigación de piscifactorías para evitar o frenar el deterioro de las poblaciones de peces.

INTRODUCTION

Several of California's marine fish stocks have declined severely over the past 70 years. Recreational and commercial fishermen have become increasingly vocal about rights to the dwindling supply of fish. In California, the concept of marine fish hatcheries was successfully promoted in the state legislature as a painless answer to this problem. A well-meaning California politician explained that instead of fighting over smaller and smaller slices of the pie, we now have the opportunity to increase the size of the pie itself. A modern technological solution to a politically difficult problem is hard to argue against. Yet I doubt that marine hatcheries are likely to solve the problem of declining fish stocks. Rather, consideration of artificial propagation is making fishery resource problems worse.

HISTORICAL PERSPECTIVE

The "hatchery solution" has a long history of attempted marine application, and from that history we should be able to learn a few lessons. Cod (*Gadus morhua*) larvae were released into the Atlantic Ocean for nearly a hundred years, beginning in the late nineteenth century. In the United States, some 50 billion cod larvae were released between 1890 and 1950, but it wasn't until 1952 that the operation was terminated due to lack of evidence that any worthwhile benefits had been obtained (Duncan and Meehan 1954).

The history of the Norwegian cod hatchery initiated by Captain Dannevig at Flødevigen (reviewed by Solemdal et al. 1984) provides further evidence that wishful thinking can postpone rational decisions almost indefinitely. The Norwegian hatchery operation was not closed until 1971, despite decades of research that failed to demonstrate any effect on the fish population. In 1911, Johan Hjort and a minority faction of a government committee issued an opinion that the question concerning the benefit from the Flødevigen hatchery was unsolvable, and that the hatchery should be discontinued. The majority of the committee advised against the hatchery's termination, but did point out that current methods needed to be replaced by unspecified "more complete" methods (cited in Solemdal et al. 1984). Ironically, the result was conversion of the Flødevigen hatchery from a privately funded operation to a government operation, which was to continue in virtually the same mode of operation for 60 more years.

It is interesting to read portions of Solemdal et al. (1984) in view of currently renewed hatchery interest in Norway. Whereas the former practice was to release early larvae, the new approach is to raise the fish to somewhat larger size and release them as juveniles; this is similar to the California plan.

> The seemingly obtuse custom of introducing a practice prior to investigating its effect, as was the convention in Flødevigen in the 1880's may in fact have been a necessity

during those pioneer days of small scientific staff and little experience. With our knowledge, experience and well established research institutions the scientific investigations should precede the practice. We are specially thinking of the mass production of cod 0-group and the possibilities of restocking depleted populations.

Though the consistency of fry production still has to be demonstrated it is obvious that mass production will be a reality within some years. The fry produced can be used either in intense farming or released into the sea as a method for population restocking. Many people have a strong belief in the latter concept, while others are more skeptical. In fact, the situation is about the same as when Captain Dannevig was applying for support in the early 1880's.

The primary difference is that today the development is mostly an official task and therefore should be both under scientific and economic control. But the American hatcheries which were also developed within the official system, show that this is not a guarantee for the proper, logical and sound development of a project. The most obvious pitfalls today are lack of knowledge by the administration, too optimistic statements by scientists quoted by mass media, the general tendency of "fashion thinking" among administrators and scientists, and probably also critical funding from outside sources, e.g. the oil industry.

These statements apply equally to the marine fish hatchery program in California. To the credit of the California program, there is an explicit research component that is supposed to examine the effectiveness of such a program. However, determining the survival rate of hatchery-produced fish requires such a large output of those fish that a hatchery program must be fully implemented in order to determine its effectiveness! Thus the ideal of investigation preceding practice may not be achievable. Yet, as history has shown, the momentum generated is very hard to stop, despite lack of evidence that the program is effective. In fact, our technology for demonstrating positive effect in the open ocean is little better than it was at the turn of the century when Hjort deemed the question unsolvable.

SCIENCE AND HATCHERY EVALUATION

The fundamental requirements for evaluating stock enhancement by means of a hatchery operation are twofold: first, we must be able to identify hatchery-produced fish in subsequent catches, and second, we must be able to identify the genes of hatchery-produced fish in subsequent wild populations. The remaining information needed to evaluate a hatchery program is relatively trivial. If a sufficient fraction of hatchery fish live long enough to be harvested, it may be possible to justify a put-and-take operation, as is often done for inland recreational species. But without the second kind of evidence, there is no way of knowing whether the resource itself is being enhanced, which is the usual stated goal of these operations. There is no reason to believe a priori that the hatchery-reared fish is capable of natural reproduction in the wild; the fact is that we just don't know, and have little chance of finding out.

As a scientific problem, the null hypothesis is not clear. We could choose either H_o:hatchery fish are not reproductively viable, or H_o:hatchery fish are reproductively viable. The extreme difficulty of testing either hypothesis suggests that the null hypothesis, whichever it is, will not be rejected. Therefore, I submit that this either is bad science or it is not science at all. Moreover, without a substantial technological breakthrough, it is fraudulent to claim that a marine hatchery program can be evaluated "scientifically."

Fortunately, such a breakthrough may have occurred. About the only conclusive way to answer these questions is to mark and count the fish that are released from the hatchery, and monitor their recapture. Physical tags or markings can pose a handicap to survival in the wild, and could bias the results; they also provide no information on reproductive success. Only through genetic marking, a technology that recently has become practically feasible, can effective reproduction be tested. A genetic strain, as well as its offspring, should be detectable by genetic fingerprinting methods. Again, development of a genetic strain requires a long time and a large investment in hatchery facilities, before the program's potential effectiveness can be determined. Although evaluating a marine hatchery program may now be feasible, it remains extremely difficult and expensive. And that very expense bodes ill for an objective accounting of cost-effectiveness.

The few cases where marine hatcheries seem to have produced recoverable fish have been associated with estuarine rather than open-ocean fisheries (e.g., Rutledge 1989). Application to a slow-growing, late-maturing, long-lived oceanic fish such as white seabass (*Atractoscion nobilis*), as is being considered in California, strains biological and economic credibility. These fish will not become vulnerable to the commercial fishery for nearly ten years, which entails a substantial discount in economic value as well as attrition by natural mortality. The recreational fishery may encounter these fish somewhat younger, and values are undoubtedly higher to this segment of the fishery, but relative fishing pressures indicate that the bulk of the catch will be taken by the commercial fishery.

Also, the main body of the white seabass resource lies south of the Mexican border. We must further discount our hatchery production by the presently unknown but potentially large fraction that migrates south to join the main body of the population where it will be unavailable to California fisheries. Ironically, the more fish that display normal behavior and migrate south, the better is our chance of enhancing the population reproductively, but the poorer is our chance of catching those fish. Only the monitoring of genetic tags can address these difficult problems.

The critical question of whether a marine hatchery will be effective is not answerable before the attempt, and is exceedingly difficult to answer even after the attempt. Meanwhile, the operation is very expensive. Moreover, the program is prone to justification by wishful thinking: history has shown that a hatchery program can generate a broad base of public and political support in the total absence of any objective evidence that it actually works.

FINAL IRONIES

Effective management of fisheries on declining natural stocks has always been difficult to obtain. In California, effective management often has been legislated only after a resource has declined to a level so low that politicians no longer fear criticism for restricting catches (e.g., sardines, Pacific mackerel, Pacific bonito). The California fisheries for white seabass have declined severely (Vojkovich and Reed 1983), and in the 1980s we seemed to be nearing the historically proven conditions for effective fishery legislation. Now the "hatchery option" has changed this pattern: discussion of legislation to manage the white seabass fishery suddenly ceased with the creation of the marine hatchery program in California. Even though this program is only intended to be exploratory, the people responsible for enacting fishery management feel that they have effectively addressed the issue, and they appear to have little interest in taking action to conserve the remainder of the natural stock.

California's hatchery *research* program is now the main factor preventing rehabilitation of the white seabass resource. This is not the first time that a research program has forestalled effective fishery management in California: CalCOFI itself is a similar case, having contributed to the final collapse of the California sardine fishery (Radovich 1982). Of course, in the present case of white seabass hatchery research, the fishing industry is not intentionally forestalling management as it was in the sardine case cited by Radovich. Yet I believe that the late John Radovich, who was a strong proponent of research on marine fish hatcheries, would be dismayed to find that a legislated program of fishery research once again has postponed effective management, and is contributing actively to collapse of another fish resource.

LITERATURE CITED

Duncan, L. M., and O. L. Meehan. 1954. Propagation and distribution of food fishes for the calendar years 1951–1952. Stat. Dig. U. S. Fish Wildl. Serv. 32, 36 pp.

Radovich, J. 1982. The collapse of the California sardine fishery: What have we learned? Calif. Coop. Oceanic Fish. Invest. Rep. 23:56–78.

Rutledge, W. P. 1989. The Texas marine hatchery program—it works! Calif. Coop. Oceanic Fish. Invest. Rep. 30:(this volume).

Solemdal, P., E. Dahl, D. S. Danielssen, and E. Moksness. 1984. The cod hatchery in Flødevigen—background and realities. Flødevigen Rapportser 1:17–45.

Vojkovich, M., and R. J. Reed. 1983. White seabass, *Atractoscion nobilis*, in California-Mexican waters: status of the fishery. Calif. Coop. Oceanic Fish. Invest. Rep. 24:79–83.

8941

THE SOUTHERN CALIFORNIA JACK MACKEREL FISHERY, AND THE AGE AND LENGTH COMPOSITION OF THE CATCH FOR THE 1972-73 THROUGH 1983-84 SEASONS

by

Janet E. Mason
Pacific Fisheries Environmental Group
Southwest Fisheries Center
National Marine Fisheries Service
P.O. Box 831
Monterey, California 93942

MARINE RESOURCES TECHNICAL REPORT NO. 58
California Department of Fish and Game
1989

INTRODUCTION

Jack mackerel, *Trachurus symmetricus*, has been an economically important species for the southern California purse seine fleet since 1947. Canneries started packing it as a substitute for Pacific mackerel,*Scomber japonicus*, and sardines,*Sardinops sagax*., during the collapse of the sardine population and the decline of the Pacific mackerel population in the late 1940's. Jack mackerel are taken by this fleet from waters near shore along the coast between Point Conception and the Mexican border, around islands in the Southern California Bight, and in some years, offshore at Tanner and Cortez banks. Schools of mackerel are sometimes species specific, but often consist of a mixture of jack mackerel, Pacific mackerel, and at times sardines. The jack mackerel caught in the purse seine fishery are primarily small, young fish which are canned at Terminal Island and Port Hueneme for human consumption and pet food.

Jack mackerel from the purse seine fleet have been sampled by the California Department of Fish and Game (CDFG) at the Terminal Island canneries since 1947. They are measured to study length frequency; their sex is recorded, and otoliths are removed for age determination. Since 1966, they have also been weighed, and gonadal maturity has been recorded. The validity of otolith age determinations for this population was explored by Knaggs and Sunada (1974), and the maturation and growth were examined by Wine and Knaggs (1975). The results of the length frequency and age studies for the 1947-48 to 1971-72 fishing seasons have been presented in a series of marine resources technical reports published by the Department of Fish and Game: Knaggs (1974a); Knaggs (1974b); Knaggs and Barnett (1975); Fleming and Knaggs (1977).

This report updates the information presented in those technical reports. It describes variations in factors affecting the jack mackerel purse seine fishery in the 1972-73 through 1983-84 seasons, and the age and length composition of jack mackerel from that period. For the purpose of this report, a season extends from August 1 to July 31 of the following calendar year. There is no closed season on jack mackerel fishing, and the species is often available year-round.

THE HISTORY OF THE FISHERY

Fluctuations in the volume of jack mackerel landings from the purse seine fishery are not necessarily indications of fluctuations in the population size. Analysis of the relative abundance of jack mackerel must take into consideration the effects of such variable factors as the economics of the fishery and the availability of the species. These fish are sold almost exclusively to the canneries, so processor orders limit the volume of the landings (MacCall and Stauffer 1983). The price paid to the fisherman by the canneries may affect landings (Figure 1), especially if there are more valuable species available.

The southern California purse seine fleet maximizes profits by fishing for a variety of pelagic schooling fish, shifting effort between these species as availability, marketability, and open fishing seasons allow. In all but three years between 1966 and 1983, northern anchovy, *Engraulis mordax*, has topped both jack and Pacific mackerel in pounds landed (Klingbeil 1984). Anchovy are fished by the same boats but with smaller mesh nets than jack mackerel, so boats are not likely to fish for both anchovy and jack mackerel in the same trip. Anchovy are not in direct competition with jack mackerel at the canneries because anchovy are reduced to fish meal. Anchovy do not command as high a price per ton as jack mackerel, but boats may shift their fishing effort between anchovy and jack mackerel when availability or marketability changes, or when commercial fishing seasons close. Anchovy fishing in southern California opens on September 15 and is limited by a quota on reduction landings. Through 1978, it closed on May 15, or as soon as the quota was filled. Since 1979, the season closure date has been June 30, and anchovy fishing has also been closed in February and March for the spawning season. Other species such as Pacific bonito, *Sarda chiliensis*, and bluefin tuna, *Thunnus thynnus*, become available to the purse seine fleet at times, and the fishermen shift their effort for weeks or months to these more profitable species.

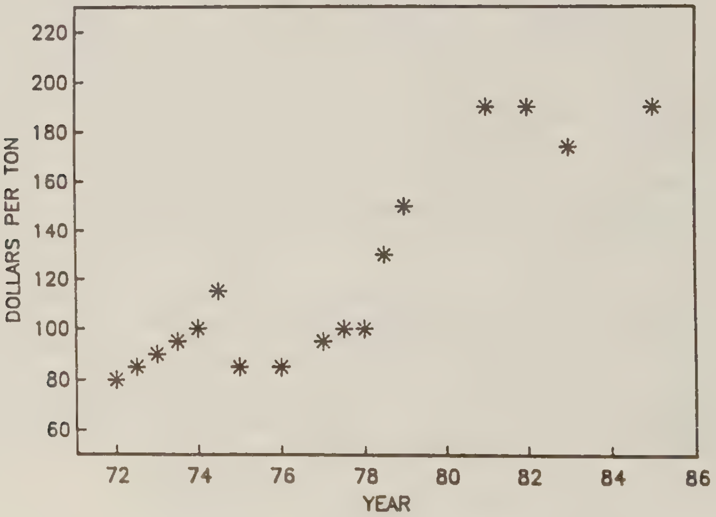


FIGURE 1. Price paid to fishermen for southern California jack mackerel in dollars per ton.

Although Pacific and jack mackerel command the same price at the canneries, Pacific mackerel availability impacts jack mackerel landings through competition for limited markets. Pacific mackerel are often more available near shore than jack mackerel, making Pacific mackerel a more profitable target. In 1982 a cannery even expressed a preference for Pacific mackerel over jack mackerel and allowed larger daily boat limits for loads of pure Pacific mackerel. This reduced the fishing effort on jack mackerel in that season.

Regulations on Pacific mackerel, in addition to the availability of the species, have affected jack mackerel landings at times. Throughout the 1950's and early '60's, jack mackerel were more abundant than Pacific mackerel. In the mid-1960's the Pacific mackerel fishery collapsed. Virtually no Pacific mackerel were caught for the next ten years. In response to the reduced Pacific mackerel biomass, a moratorium on that species went into effect in August 1970. To minimize the negative impact a recovering Pacific mackerel population might have on the jack mackerel fishery, it allowed a mixed load tolerance of up to 18 percent Pacific mackerel in loads of jack mackerel. By 1977 the percentage of Pacific mackerel in mixed catches exceeded this limit and began to seriously interfere with the landing of jack mackerel (Klingbeil 1983). When the spawning biomass was assessed at over 10,000 tons in 1978, the moratorium was lifted, and a quota system on Pacific mackerel was implemented. When a season's quota was filled, "interseason" regulations took effect, which restricted the percentage of Pacific mackerel that could be landed with jack mackerel until fishing on the next season's quota began.

THE FISHERY, 1972-73 THROUGH 1983-84 SEASONS

Factors affecting the jack mackerel landings varied during the 1972-73 through 1983-84 seasons. This review of factors for that period is based on the Reviews of the Pelagic Wet-Fisheries for 1972 through 1984 in the Cal COFI Reports (volumes XVIII- XXVI).

The 1972-73 season started with high landings of jack mackerel in August and September, followed by a shift in fishing effort to Pacific bonito, and bluefin tuna, which were available in a warm water influx during the fall of 1972. Bad weather from late December through March greatly reduced the jack mackerel catch during those months, and fish were available only sporadically in June and July (Table 1).

Jack mackerel landings during the 1973-74 season hit the lowest level since the 1954-55 season, due perhaps to increased fuel costs, poor weather, and readily available anchovy, bluefin tuna and bonito. In January 1974, the largest cannery taking jack mackerel at Terminal Island burned down, substantially reducing daily mackerel orders for the fleet.

In the 1974-75 season, the availability of anchovy, bluefin tuna and bonito again diverted effort from mackerel. High fuel costs and the scarcity of jack mackerel near shore, along with reduced cannery orders resulting from the burned cannery, contributed to this season's low jack mackerel landings. They were only slightly higher than the previous season's.

The 1975-76 season showed an increased availability of jack mackerel near shore, good weather, and increased cannery orders. As a result, landings for the season were higher than in the previous season in spite of a lower price paid to fishermen.

Jack mackerel continued to be available near shore in the 1976-77 season. In February, the cannery destroyed by fire in 1974 reopened, and another cannery began processing jack mackerel for the first time. Jack mackerel availability was up, while anchovy and bluefin tuna availabilities were down, concentrating effort on jack mackerel. In addition, the southern California fleet was encouraged to take more jack mackerel because of possible future allocations of underutilized species to foreign fleets, resulting in the highest jack mackerel landings in 12 years. Catches might have been even higher if not for the presence of Pacific mackerel in excess of the allowed 18 percent, mixed with the jack mackerel schools in May. Emergency legislation was passed in June which increased the allowable percentage of Pacific mackerel to 40 percent by weight, and allowed pure loads of Pacific mackerel of 3 tons or less.

Depressed market conditions from August through October of 1977 reduced the cannery orders and slowed the harvest of mackerel until November in the 1977-78 season. A 5,000-ton Pacific mackerel quota was set in January, and daily limits were imposed on boats landing high percentages of Pacific mackerel. The quota was filled by March 10, after which mixed mackerel landings could not contain more than 18 percent Pacific mackerel by weight. A dispute between boat owners, fishermen's unions, aerial spotters, and canneries stopped fishing from April to early July, reducing catches; however, this was also the period of restricted Pacific mackerel harvest after the quota was met, and both species were reportedly unavailable for most of this period. As a result, the jack mackerel catch was down from the previous season's high landings. Urgency legislation was passed allowing Pacific mackerel fishing to resume on July 10 until the revised quota was filled on September 18 under new tolerance limits (pure loads up to 3 tons and larger loads up to 50 percent Pacific mackerel by number).

Jack mackerel were highly available in the fall of 1978, and landings were excellent through December, but dropped much lower for the rest of the 1978-79 season. Pacific mackerel fishing opened on October 1, 1978. Jack mackerel catches may have been reduced by a shift in effort towards Pacific mackerel, which was more available near shore. Changes in the regulations allowed larger loads of "pure" (more than 50 percent) Pacific mackerel after January 22, and as the noticeably abundant 1978 Pacific mackerel year class was recruited to the fishery the Pacific mackerel catch increased. Availability of anchovies in the spring diverted effort from both jack and Pacific mackerel until June when the anchovy fishery closed. Effort then returned to Pacific and jack mackerel until July 20, when the Pacific mackerel quota was filled.

In the 1979-80 season, jack mackerel slipped from dominating total mackerel landings, to composing less than one third of the catch. After the Pacific mackerel quota was filled in late July 1979, fishing on both species virtually stopped until the new Pacific mackerel quota opened in October (Klingbeil1983). Landings continued to be low for a few weeks as effort was directed towards tuna. Jack mackerel did not dominate total mackerel landings until after early February, when catch restrictions went into effect on Pacific mackerel. Pacific mackerel regulations were again modified after the quota was filled in May 1980. A new season starting date of July 1 was established for the Pacific mackerel quota, and the incidental catch rate was increased.

Pacific mackerel again dominated jack mackerel in the 1980-81 season landings. Fishing for anchovy, bluefin tuna and bonito diverted some fishing effort away from mackerel. The Pacific mackerel quota opened on July 1 and was filled by September 19. Pacific mackerel fishing was reopened on January 20, 1981, after the biomass estimate was reevaluated, and remained open and unrestricted for approximately one month until the new quota was reached. The shift in dominance from jack to Pacific mackerel in spite of restrictions must be attributed to the increased population of the species and its availability.

The 1981-82 season was again led by Pacific mackerel. The Pacific mackerel quota opened on July 1 with Pacific mackerel dominating the catch through January. Cannery limits on orders restricted landings during the winter. The quota on Pacific mackerel was filled on March 6, and "interseason" restrictions of 50 percent incidental catch in loads greater than 3 tons went into effect. Catches were over half jack mackerel from February through June, but Pacific mackerel still dominated the landings for the season.

Landings were led alternately by jack and Pacific mackerel throughout the 1982-83 season. Jack mackerel was more available than Pacific mackerel in the summer and fall of 1982; however in November, one cannery established higher daily limits for boats delivering pure Pacific mackerel, and Pacific mackerel began to dominate the catch. Bad weather kept catches down in February and March of 1983. In April, the weather improved and landings picked up. Jack mackerel returned to dominate the catch for the month of April; however, the Pacific mackerel quota was not met until June 23, 1983, and Pacific mackerel finished the season strong, with higher total landings than jack mackerel.

The 1983-84 season was an unusual one because it occurred during a major El Nino. Jack mackerel became largely unavailable off southern California during August and remained so through December. Pacific mackerel were caught in August and September but had disappeared from southern California by late October. The fleet moved up to Monterey where 62 percent of December's Pacific mackerel was caught. The jack mackerel catch was better off central California as well. Fish landed in Monterey are not included in the tables that follow; however, some boats caught fish in the Monterey area and returned to unload at Terminal Island, and those fish are included in the southern California landings. Fishing activity remained centered around Monterey until late January when Pacific mackerel became available off the Santa Barbara Channel Islands. Jack mackerel were still unavailable off southern California and made it hard to meet "interseason" restrictions of no more than 50 percent Pacific mackerel after the quota was met in early February. The Pacific mackerel quota was reopened for about a week in April, in May, and in June primarily to alleviate financial hardship to the fishermen due to the scarcity of jack mackerel. While the specific effects of El Nino on mackerel are not known, the 1983 event did alter the availability of jack and Pacific mackerel off southern and central California.

In summary, the factors effecting jack mackerel landings fell into four general categories: i) availability of other species; ii) availability near shore; iii) weather; and iv) market conditions. The effort directed toward jack mackerel was reduced in some seasons by the availability of the following species: bonito and bluefin tuna in 1972, 1973, 1974 and 1980; anchovy in 1973, 1974, 1977 and 1980; and Pacific mackerel from 1977 through 1983. Increased fuel cost in 1973 and 1974 seasons kept boats nearer shore where jack mackerel were not available. (Good availability nearshore produced high landings of jack mackerel in the 1975 and 1976 seasons). Several months of bad weather slowed the jack mackerel catch in the 1972 and 1982 seasons. Depressed market conditions in the 1977 season reduced cannery orders for jack mackerel. Catches of jack mackerel were greatly reduced during the 1983 El Nino because both jack and Pacific mackerel were unavailable in southern California.

METHODS

Jack mackerel landed in southern California, between Point Conception and the Mexican border, were sampled at the Terminal Island canneries by CDFG. Two sampling plans were used during the 1972 to 1984 period. From 1972-73 through 1977-78 a stratified random sampling plan was used. A stratum consisted of 5,000 tons (4,500 MT) of jack mackerel, based on estimated landings. Forty random samples were taken per stratum. A list of random numbers was prepared and sequenced in advance; as the cumulative tonnage of landings met or exceeded each of these numbers, the boat unloading was sampled, even if that meant more than one sample was taken from some boatloads. Samples consisted of approximately 5 pounds (2.27 kg) of jack mackerel, to the nearest fish. Each fish in a sample was weighed to the nearest gram, measured to the nearest millimeter fork length (FL), and had its otoliths removed for age determination (Fleming and Knaggs 1977).

Historically, jack mackerel, Pacific mackerel and sardines have often been caught together in mixed schools. The stratified sampling plan, however, was developed for the single species jack mackerel fishery which occurred during the late 1960's and early 1970's when Pacific mackerel and sardines were rare. The plan was modified in 1978 when Pacific mackerel landings increased to more than 10 percent of the total catch . The modified plan was used from the 1978-79 through the 1983-84 season. Boatloads to be sampled were still chosen randomly within a stratum; however, the stratum now consisted of 5,000 tons of "mixed mackerel" with varying percentages of jack mackerel, Pacific mackerel, and sardines. When a boatload was selected for sampling, each mackerel species estimated to constitute at least 5 percent of the load was sampled, and sardines were sampled if they comprised at least 1 percent of the load. Therefore, the number of jack mackerel samples in a stratum varied, and the probability of sampling a boatload was no longer proportional to the weight of jack mackerel landed.

Estimates of the species composition of the catch were made as boats unloaded at Terminal Island. Two methods were used.[1] The first method was used on about 36 percent of the boats by Wildlife Protection personnel from CDFG, who sampled mixed mackerel landings to enforce Pacific mackerel regulations. They recorded the number of fish and the combined weight of each species per 30 pound sample. Samples were taken at a rate of one sample for approximately ten tons of landings. CDFG biologists, who carried out the biological sampling program, used a second system. They made a visual estimate of the species composition during the unloading process for about 75 percent the boatloads. Estimates of the percent of each species by weight in the catch were made with at least one of these methods for 80 percent of the mixed species boatloads after 1975. Jack mackerel landings were calculated on a monthly basis by applying the proportional species composition of the observed landings to the total mixed mackerel landings for southern California (weighed samples were used whenever available), (Table 1).

Numbers of fish landed for each season were calculated by month, as in Knaggs (1974a) for the 1947-48 to 1956-57 seasons, instead of by stratum, as in Fleming and Knaggs (1977) for the 1967-68 to 1971-72 seasons, because landings by stratum were not available for all of this period, and because the 5,000 ton stratum was no longer a consistent unit of jack mackerel landings. Monthly average weights by year class of sampled fish were applied to the total pounds landed for the month to calculate the approximate number of fish landed. During months with no sampling, the average weight of fish by year class for fish sampled during that season was applied.

Age determinations were made on whole otoliths by CDFG biologists under a cooperative National Marine Fisheries Service (NMFS)/CDFG program with procedures described by Knaggs and Sunada (1974). Numbers of otolith pairs read for each of the 1972-73 to 1983-84 seasons ranged between 922 and 3293 (Tables 2-13).

The estimated numbers of jack mackerel by length group (Tables 14 and 15), and the numbers and pounds by age group (Tables 16 and 17), were calculated for each month with computer programs. Monthly values were summed to give season totals. To be consistent with reports from previous years, a season starting date of August 1st was used for all tables in this report. This groups fish together by year class within the season, and is consistent with the way ages were analyzed in the previous report, Fleming and Knaggs (1977).

The landings by age-group for year classes from Fleming and Knaggs (1977) were expanded for the 1967-68 through 1971-72 seasons to include all southern California landings between Point Conception and the Mexican border, instead of only Terminal Island landings (Tables 18 and 19). This makes the time series of landings from 1947-48 to 1983-84 consistent in landing area, simplifying comparison of year class estimates from different seasons.

---

[1] Patricia Wolf, unpublished. State of California Department of Fish and Game, Field and Laboratory Sampling Methods for Pacific Mackerel, Jack Mackerel, Sardine and Anchovy. California Department of Fish and Game, Pelagic Fisheries, Long Beach, CA. October, 1987.

AGE COMPOSITION

The jack mackerel population has exhibited wide variations in the relative strength of different year classes in the fishery. In the 1940's and '50's, year classes were either strongly or weakly represented in the fishery. Strongly represented jack mackerel year classes occurred in 1947, 1952, and 1958 (Figure 2). Each of these year classes contributed over 250 million fish, and the 1958 year class, with over 400 million fish, was the most abundant year class recorded in the history of the fishery. Fish from each of these strongly represented year classes contributed significantly to the fishery for five or more fishing seasons. These three strong year classes were separated by strings of four or five weakly represented year classes which contributed between 40 million and 150 million fish to the fishery. The extremely strong 1958 year class was followed by two relatively strong year classes in 1959 and 1960. Both of these year classes contributed about 250 million fish apiece to the fishery. These were followed by five moderately represented year classes in 1961 through 1965, each contributing only about 100 million to 160 million fish. Another group of relatively strong year classes, 1966 through 1970, each contributed about 200 million fish or more, with 1967 and 1970 being the strongest. However, since the 1966 to 1970 year classes were caught mainly as young-of-the-year and one-year-olds, they produced only moderate landing weights (Table 19).

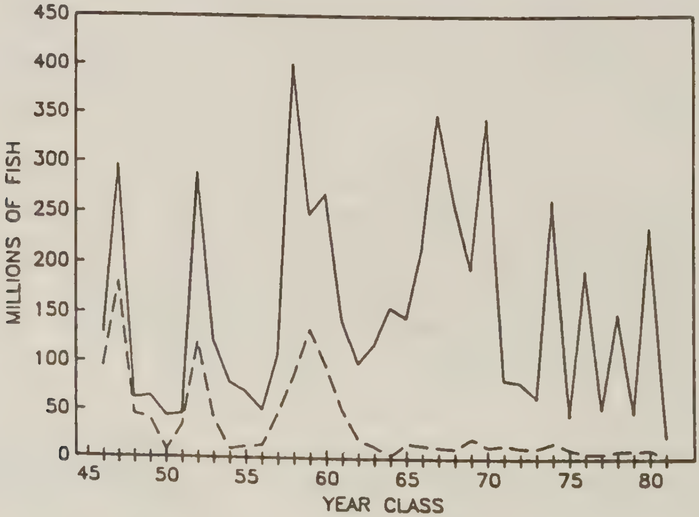


FIGURE 2. Total jack mackerel by year class from southern California landings for the 1947-48 to 1983-84 seasons are indicated by the solid line. Fish caught at ages older than 2 are indicated by the dashed line.

The seasons updated by this report, 1972-1983, can be separated into three types based on the age composition of the catch . The catch was not dominated by a single year class, but was spread among young-of-the year to three-year-old fish for three seasons, 1972-73 through 1974-75 (Table 16). This was followed by eight seasons, 1975-76 to 1982-83, during which single year classes in the one- to three-year-old range dominated each season's landings (Tables 16 and 17). The final season occurred during the major El Nino in 1983; jack mackerel were scarce in southern California, and the catch was divided between two and three-year-old fish.

The 1973-74 and 1974-75 seasons had the lowest season's landings since 1954-55, apparently due to poor year classes in 1971 to 1973 which provided less than 90 million fish apiece to the fishery (Figure 2).

The 1974 to 1981 period is marked by a series of alternating strong and weak year classes (Figure 2). The 1974, 1976, 1978, and 1980 year classes were relatively strong, each contributing over 150 million fish and more than 60 million pounds to the fishery, while 1975, 1977, 1979 and 1981 each contributed less than 60 million fish and less than 25 million pounds (Tables 18 and 19). Each of the strong year classes dominated the fishery for two years, as one- and two-year-olds.

A scarcity of fish in southern California during the 1983 El Nino, along with weak year classes in 1981 and 1982, led to record low landings in the 1983-84 season (Table 17). The 1980 year class remained dominant in this season.

The most noticeable change in the age composition of the jack mackerel landings has been a marked decrease in the average age since the 1940's and 50's (Figure 2). In the 1939 to 1961 year classes, fish of age 3 and older accounted for 45 percent of the fish caught, whereas from the 1962 year class on, they have composed less than 10 percent of the fishery.

LITERATURE CITED

Bedford, D., S. Crooke, T. Jow, R. Klingbeil, R. Read, J. Spratt, and R. Warner. 1982. Review of some California fisheries for 1980 and 1981. CalCOFI Rep 23:8-14.

Bedford, D., T. Jow, R. Klingbeil, R. Read, J. Spratt, and R. Warner. 1983. Review of some California fisheries for 1982. CalCOFI Rep 24:6-10.

Fleming, E. R., and E. H. Knaggs. 1977. The southern California jack mackerel fishery and age, length and sex composition of the catch for the 1967-68 through 1971-72 seasons. Calif. Dep. Fish and Game, Mar Res Tech Rep 37:1-44.

Klingbeil, R. A. 1977a. Review of the pelagic wet fisheries for 1976 with notes on the history of these fisheries. CalCOFI Rep 20:6-9.

Klingbeil, R. A. 1977b. Review of the pelagic wet fisheries for 1977. CalCOFI Rep 20:10-12.

Klingbeil, R. A. 1983. Pacific mackerel: A resurgent resource and fishery of the California current. CalCOFI Reports 24: 35-45.

Klingbeil, R. A. 1984. Review of some California fisheries for 1983. CalCOFI Rep 25:7-15.

Klingbeil, R. A. 1985. Review of some California fisheries for 1984. CalCOFI Rep 26:9-16.

Klingbeil, R. A., J. S. Sunada and J. D. Spratt.1980. Review of the pelagic wet fisheries for 1978 and 1979. CalCOFI Rep 21:8-11.

Knaggs, E. H. 1974a. The southern California jack mackerel fishery and age composition of the catch for the 1947-48 through 1956-57 seasons. Calif. Dep. Fish and Game, Mar Res Tech Rep 22:1-47.

Knaggs, E. H. 1974b. The southern California jack mackerel fishery and age composition of the catch for the 1957-58 through 1961-62 seasons. Calif. Dep. Fish and Game, Mar Res Tech Rep 24:1-25.

Knaggs, E. H., and J. S. Sunada. 1974. Validity of otolith age determinations for jack mackerel, *Trachurus symmetricus,* from the Southern California Bight area. Calif. Dep. Fish and Game, Mar Res Tech Rep 21:1-11.

Knaggs, E. H., and P. A. Barnett. 1975. The southern California jack mackerel fishery and age composition of the catch for the 1962-63 through 1966-67 seasons. Calif. Dep. Fish and Game, Mar Res Tech Rep 28:1-28.

Lehtonen, P. 1976. Review of the pelacic wet-fisheries for 1974. CalCOFI Rep 18:21-22.

MacCall, A. D., and G. D. Stauffer. 1983. Biology and fishery potential of jack mackerel (*Trachurus symmetricus*). CalCOFI Rep 24:46-56.

Sunada, J. S. 1977. Review of the pelacic wet-fisheries for 1975. CalCOFI Rep 19:19-20.

Wine, V. L., and E. H. Knaggs. 1975. Maturation and growth of jack mackerel, *Trachurus symmetricus.* Calif. Dep. Fish and Game, Mar Res Tech Rep 32:1-26.

Wine, V. L. 1976. Review of the pelacic wet-fisheries for 1973. CalCOFI Rep 18:19-20.

TABLE 1. Southern California jack mackerel landings in thousands of pounds.

	Season										
Month	1972-73	1973-74	1974-75	1975-76	1976-77	1977-78	1978-79	1979-80	1980-81	1981-82	1982-83	1983-84
August	9888	1786	4501	1422	4596	4010	12712	3224	3800	1664	5142	2028
September	13416	224	638	6245	2296	2224	8615	758	4403	1258	8495	1
October	642	3135	3412	8221	1695	3331	9641	1808	6861	513	6154	141
November	2146	1167	3339	4902	3111	10078	6784	6059	2933	1450	2074	502
December	981	259	366	7705	3117	5372	1763	3428	6499	2131	387	223
January	253	1279	427	6260	7967	2885	910	5286	2720	3404	2300	1306
Febuary	425	1582	2851	6102	5106	2570	795	1620	3644	7266	893	358
March	473	199	848	4503	8144	6492	1217	936	6364	7191	753	1358
April	690	949	827	2936	13944	3925	2955	1684	6653	4006	9956	2737
May	1444	3115	1194	2761	6625	658	2846	2547	2011	1534	8893	3777
June	6843	629	1237	2576	11717	650	889	1224	383	2757	3855	1107
July	3429	5426	860	4820	11664	11267	10410	6655	1769	9417	4148	198
Totals	40630	19750	20500	58453	79982	53462	59537	35229	48040	42591	53050	13736

TABLE 2. Length frequencies for 1972-73 season by 5 mm groups.

mm FL	Total sampled	Age groups 0	I	II	III	IV	V	VI	VII	VIII
130	8	8								
135	11	11								
140	20	20								
145	15	15								
150	13	13								
155	9	9								
160	6	6								
165	9	9								
170	23	23								
175	22	22								
180	32	32								
185	39	38	1							
190	40	38	2							
195	43	36	7							
200	79	64	14	1						
205	131	92	33	6						
210	164	73	83	8						
215	191	58	114	19						
220	166	19	115	30	2					
225	162	7	118	37						
230	144	3	92	49						
235	129		66	54	9					
240	114		46	64	4					
245	134		35	87	12					
250	105		14	76	14	1				
255	126		9	93	22	2				
260	126		7	94	24	1				
265	131		3	85	40	3				
270	98			53	43	2				
275	91		1	41	44	5				
280	87			20	58	9				
285	50			8	37	5				
290	40			7	27	6				
295	18			2	11	5				
300	17				9	7	1			
305	16				7	9				
310	6				2	3	1			
315	1					1				
320	3					1	1	1		
325	3				1	1	1			
330	1						1			
335	1						1			
340	1							1		
Total	2625	596	760	834	366	61	6	2	0	0
Mean FL	235	193	226	252	275	291	323	332	0	0

TABLE 3. Length frequencies for 1973-74 season by 5 mm groups.

mm FL	Total sampled	Age groups 0	I	II	III	IV	V	VI	VII	VIII
130										
135	3	3								
140	4	4								
145	4	4								
150	8	8								
155	18	18								
160	26	26								
165	39	38	1							
170	33	33								
175	41	35	6							
180	55	47	8							
185	53	43	10							
190	48	34	14							
195	42	23	19							
200	43	12	29	2						
205	55	17	34	4						
210	45	13	27	5						
215	87	12	56	19						
220	73	11	48	14						
225	61	5	39	17						
230	45	1	33	10	1					
235	35	1	23	11						
240	48		20	27	1					
245	34		8	23	3					
250	32		5	21	6					
255	22			18	4					
260	29		4	16	8	1				
265	44			19	24	1				
270	37		1	17	18	1				
275	26			10	15		1			
280	22			2	18	2				
285	15			2	10	3				
290	17				16	1				
295	11				5	6				
300	18				4	10	4			
305	11					10	1			
310	8					4	3	1		
315	12					5	4	3		
320	11					5	5	1		
325	17					3	11	3		
330	4						2	2		
335	4					1	2	1		
340	1								1	
345	3							3		
350										
355										
360										
365										
370	1						1			
375										
Total	1245	388	385	237	133	53	34	14	1	0
Mean FL	226	183	218	246	276	305	321	329	340	0

TABLE 4. Length frequencies for 1974-75 season by 5 mm groups.

mm FL	Total sampled	Age groups 0	I	II	III	IV	V	VI	VII	VIII
130										
135										
140										
145										
150										
155										
160	2	2								
165	4	4								
170	5	5								
175	17	17								
180	34	34								
185	33	33								
190	19	19								
195	25	25								
200	17	16	1							
205	15	8	6	1						
210	22	7	13	1		1				
215	26		21	5						
220	22		13	9						
225	65		36	29						
230	76		23	52	1					
235	108		14	85	9					
240	108		13	84	11					
245	95		6	76	13					
250	39		2	31	5	1				
255	29			17	12					
260	28			14	13	1				
265	14			6	7	1				
270	12			2	10					
275	12			1	10	1				
280	7				3	3	1			
285	9				4	5				
290	9				1	8				
295	13				3	9	1			
300	16				1	11	4			
305	9					8	1			
310	8					5	3			
315	10				1	4	5			
320	8					2	5	1		
325	3						3			
330	1							1		
335	1								1	
340										
345										
350										
355										
360										
365										
370										
375										

TABLE 4. Continued.

mm FL	Total sampled	Age groups								
		0	I	II	III	IV	V	VI	VII	VIII
380										
385	1							1		
Total	922	170	148	413	104	60	23	3	1	0
Mean FL	237	189	227	241	261	297	313	346	335	0

TABLE 5. Length frequencies for 1975-76 season by 5 mm groups.

mm FL	Total sampled	Age groups 0	I	II	III	IV	V	VI	VII	VIII
130										
135										
140										
145										
150										
155										
160										
165	1		1							
170	2		2							
175	7		7							
180	7		7							
185	14		14							
190	9		9							
195	26		26							
200	45		45							
205	71		71							
210	143		143							
215	256		254	2						
220	351		345	6						
225	343		325	18						
230	246		211	35						
235	202		144	53	5					
240	143		87	48	8					
245	96		49	44	3					
250	83		32	46	5					
255	78		30	39	8	1				
260	67		16	40	11					
265	56		7	30	15	4				
270	37		4	9	16	8				
275	22			7	13	2				
280	35		3	6	17	8	1			
285	30				15	13	2			
290	39			1	17	20	1			
295	44				19	25				
300	32				9	19	3	1		
305	31			1	8	21	1			
310	13				5	5	3			
315	17				3	10	3	1		
320	6					3	3			
325	11					4	7			
330	7			1	1		4		1	
335	5					1	4			
340	1					1				
345	4						1	2	1	
350										
355	3					1	1	1		
360										
365	1								1	
370	2							2		
375										

TABLE 5. Continued.

mm FL	Total sampled	Age groups								
		0	I	II	III	IV	V	VI	VII	VIII
380	1									1
385	1								1	
Total	2588	0	1832	386	178	146	34	7	4	1
Mean FL	238	0	225	249	279	298	320	345	358	380

TABLE 6. Length frequencies for 1976-77 season by 5 mm groups.

mm FL	Total sampled	Age groups 0	I	II	III	IV	V	VI	VII	VIII
130										
135										
140	2	2								
145	1	1								
150	15	15								
155	29	29								
160	32	32								
165	51	51								
170	37	37								
175	42	42								
180	55	55								
185	66	66								
190	58	58								
195	39	39								
200	47	45	2							
205	55	51	4							
210	69	67	2							
215	71	62	9							
220	74	52	22							
225	60	31	29							
230	62	18	41	3						
235	53	9	43	1						
240	32	1	30	1						
245	32	3	24	5						
250	35		22	13						
255	43		20	21	2					
260	88		16	69	3					
265	148		19	125	4					
270	207		21	178	8					
275	222		17	199	6					
280	232		12	205	15					
285	245		13	222	10					
290	216		6	200	10					
295	212		12	183	17					
300	194		8	165	21					
305	158		6	136	16					
310	100		9	84	7					
315	80		3	66	11					
320	49		1	34	12	2				
325	30		4	19	7					
330	17		1	10	5	1				
335	16			6	9	1				
340	5			3	2					
345	3			2		1				
350	3				1	2				
355	2					1	1			
360										
365	1					1				
370										
375	2				1	1				

TABLE 6. Continued.

mm FL	Total sampled	Age groups								
		0	I	II	III	IV	V	VI	VII	VIII
380										
385										
390										
395	1						1			
400										
405										
410										
415										
420										
425	1					1				
430										
435										
440										
445										
480	1									1
Total	3293	766	396	1950	167	11	2	0	0	1
Mean FL	264	195	254	289	302	354	375	0	0	481

TABLE 7. Length frequencies for 1977-78 season by 5 mm groups.

mm	Total	Age groups								
FL	sampled	0	I	II	III	IV	V	VI	VII	VIII
130										
135	1	1								
140										
145	3	3								
150	4	4								
155	11	11								
160	14	14								
165	25	25								
170	14	14								
175	13	12	1							
180	10	8	2							
185	25	12	13							
190	27	11	16							
195	34	12	22							
200	47	23	24							
205	42	18	24							
210	43	10	33							
215	59	11	48							
220	82	16	66							
225	117	10	107							
230	231	3	225	3						
235	281	7	273	1						
240	283	6	265	12						
245	240	4	232	4						
250	219	4	196	19						
255	169	1	149	19						
260	101		82	18	1					
265	84		66	18						
270	87		66	20	1					
275	52		34	18						
280	49		21	23	5					
285	37		5	25	7					
290	42		4	29	9					
295	40		2	21	17					
300	67		1	28	35	3				
305	55			13	41	1				
310	63			22	41					
315	49			10	38	1				
320	34			3	26	5				
325	24			3	19	2				
330	25			2	20	3				
335	8				5	3				
340	12				4	7	1			
345	7			1	3	3				
350	5				3	1	1			
355	3				2	1				
360										
365	1						1			
370	1				1					
375										

TABLE 7. Continued.

mm FL	Total sampled	Age groups 0	I	II	III	IV	V	VI	VII	VIII
380										
385										
390										
395										
400										
405										
410										
415										
420										
425	1							1		
Total	2841	240	1977	312	278	30	3	1	0	0
Mean FL	251	195	242	283	313	331	353	428	0	0

TABLE 8. Length frequencies for 1978-79 season by 5 mm groups.

mm FL	Total sampled	Age groups 0	I	II	III	IV	V	VI	VII	VIII
130										
135										
140										
145										
150	2	2								
155	1	1								
160	3	3								
165	1	1								
170	7	7								
175	13	12	1							
180	16	16								
185	22	22								
190	32	30	2							
195	42	40	2							
200	28	25	3							
205	39	34	5							
210	40	27	13							
215	52	37	15							
220	58	44	13	1						
225	66	42	23	1						
230	81	40	40	1						
235	84	15	65	4						
240	62	6	50	6						
245	88	4	65	19						
250	84	1	55	28						
255	100	1	38	60	1					
260	117		33	81	3					
265	173		33	136	4					
270	240	2	28	205	5					
275	186		6	176	4					
280	158		1	146	11					
285	121		1	111	9					
290	90		8	59	22	1				
295	44		1	34	9					
300	30		1	12	17					
305	23		1	10	10	2				
310	21			9	7	5				
315	22			9	11	2				
320	26			1	11	14				
325	17				11	5	1			
330	19				7	11	1			
335	19				6	12	1			
340	17				5	6	6			
345	13				1	8	4			
350	11				1	2	7	1		
355	6				1	1	3	1		
360	5					2	3			
365	3					1	2			
370	4					2	2			
375										

TABLE 8. Continued.

mm FL	Total sampled				Age groups					
		0	I	II	III	IV	V	VI	VII	VIII
380										
385										
390	1						1			
Total	2287	412	503	1109	156	74	31	2	0	0
Mean FL	262	210	246	275	304	333	352	355	0	0

TABLE 9. Length frequencies for 1979-80 season by 5 mm groups.

mm FL	Total sampled	Age groups								
		0	I	II	III	IV	V	VI	VII	VIII
130										
135	2	2								
140										
145	2	2								
150	10	10								
155	12	12								
160	7	6	1							
165	15	15								
170	7	7								
175	15	11	4							
180	9	7	2							
185	22	13	9							
190	21	16	5							
195	18	12	6							
200	27	15	12							
205	30	23	7							
210	40	21	19							
215	46	24	22							
220	87	25	62							
225	127	26	101							
230	174	10	161	3						
235	240	14	223	3						
240	323	5	308	9	1					
245	286	2	271	13						
250	196	1	180	15						
255	148	2	127	19						
260	90	1	73	16						
265	78	1	59	18						
270	71		48	22	1					
275	47		29	18						
280	38		14	19	5					
285	26		10	13	3					
290	15			11	4					
295	17			9	8					
300	14			5	9					
305	17			5	11	1				
310	14			4	9	1				
315	13				13					
320	9				8	1				
325	13				8	3	2			
330	5				3	2				
335	8				1	4	3			
340	3					1	2			
345	3					1	2			
350	2						2			
355	2						2			
360	1					1				
365	1					1				
Total	2351	283	1753	202	84	16	13	0	0	0
Mean FL	244	202	244	271	308	334	343	0	0	0

TABLE 10. Length frequencies for 1980-81 season by 5 mm groups.

mm FL	Total sampled	Age groups 0	I	II	III	IV	V	VI	VII	VIII
130										
135										
140										
145	1	1								
150	2	2								
155	6	6								
160	12	12								
165	26	26								
170	47	47								
175	75	75								
180	99	99								
185	127	127								
190	117	117								
195	115	115								
200	82	77	5							
205	53	49	4							
210	48	39	9							
215	19	9	10							
220	23	12	11							
225	17	3	14							
230	19	1	17	1						
235	26	2	22	2						
240	36	1	30	5						
245	61	1	47	13						
250	68		57	11						
255	86		58	28						
260	92		52	40						
265	93		45	48						
270	108		33	75						
275	100		17	81	2					
280	146		7	134	4	1				
285	145		2	143						
290	177			169	8					
295	126			119	7					
300	79			71	8					
305	50			39	11					
310	27			17	10					
315	11			3	7	1				
320	9			1	3	4	1			
325	7			2	2	3				
330	2				2					
335	3			1	1	1				
340	4					4				
345	6				1	5				
350	5				1	3	1			
355	3						2	1		
360	5					3	2			
365	2					1	1			
370	3					1	2			
375	2						2			

TABLE 10. Continued.

mm	Total				Age groups					
FL	sampled	0	I	II	III	IV	V	VI	VII	VIII
380	1						1			
385	5						2	2	1	
390	7					3	2	2		
395	2							2		
400										
405	1								1	
410	2							1	1	
415	1								1	
420										
425										
430										
435										
440	1								1	
Total	2390	821	440	1003	67	30	16	8	5	0
Mean FL	249	191	252	285	306	346	370	390	413	0

TABLE 11. Length frequencies for 1981-82 season by 5 mm groups.

mm FL	Total sampled	Age groups 0	I	II	III	IV	V	VI	VII	VIII
130										
135										
140										
145	1	1								
150	4	4								
155										
160	1	1								
165										
170										
175	4	4								
180	12	12								
185	9	9								
190	13	13								
195	20	19	1							
200	26	2	24							
205	34		34							
210	91	5	86							
215	130	2	127	1						
220	136	2	134							
225	129		128	1						
230	168		168							
235	179		177	2						
240	209		206	3						
245	219		210	9						
250	173		166	7						
255	153		136	17						
260	113		95	18						
265	75		56	19						
270	49		23	25	1					
275	24		7	16	1					
280	29		4	23	2					
285	27		2	21	4					
290	43		1	31	11					
295	32		1	17	13	1				
300	32			16	15	1				
305	33			10	22	1				
310	33			1	31	1				
315	29			3	24	2				
320	35			1	27	6	1			
325	28				23	4	1			
330	20				15	4	1			
335	17				8	9				
340	10				3	6	1			
345	10				3	7				
350	3				1	1	1			
355	3				1	2				
360	7				2	3	2			
365	1				1					
370										
375	1						1			

TABLE 11. Continued.

mm FL	Total sampled	Age groups 0	I	II	III	IV	V	VI	VII	VIII
380										
385	4					1	2	1		
390	2						2			
395	1						1			
400	2					1	1			
405	1								1	
410										
415	1							1		
420										
425										
430	1						1			
Total	2377	74	1786	241	208	50	15	2	1	0
Mean FL	251	190	239	279	316	338	371	403	408	0

TABLE 12. Length frequencies for 1982-83 season by 5 mm groups.

mm FL	Total sampled	Age groups 0	I	II	III	IV	V	VI	VII	VIII
130										
135										
140										
145										
150										
155										
160										
165										
170										
175	3	3								
180	2	2								
185	4	4								
190	3	3								
195	2	2								
200	1		1							
205	7	3	4							
210	12	4	8							
215	25	5	20							
220	28	7	21							
225	29	5	24							
230	46	4	35	7						
235	36	1	14	21						
240	77	1	24	52						
245	157		18	138	1					
250	235		10	222	3					
255	296		25	266	5					
260	249		11	228	10					
265	215		6	203	6					
270	206		2	187	17					
275	188			174	14					
280	155		1	143	11					
285	113		1	96	16					
290	66			51	15					
295	42			29	13					
300	33			16	15	2				
305	10			5	4	1				
310	5				5					
315	6				5	1				
320	6				4	1		1		
325	2				1	1				
330	3					3				
335	4					2	2			
340	2				1		1			
345	2					1	1			
350	3					1	2			
355										
360	1							1		
365	2					1	1			
370										
375										

TABLE 12. Continued.

mm FL	Total sampled	0	I	II	Age groups III	IV	V	VI	VII	VIII
380	1					1				
Total	2277	44	225	1838	146	15	7	2	0	0
Mean FL	264	210	237	266	286	333	348	342	0	0

TABLE 13. Length frequencies for 1983-84 season by 5 mm groups.

mm FL	Total sampled	0	I	II	Age groups III	IV	V	VI	VII	VIII
130										
135										
140										
145										
150										
155										
160										
165										
170										
175	1	1								
180	2	1	1							
185	3	1	2							
190	1		1							
195	9	4	5							
200	10	5	5							
205	9	1	8							
210	6		6							
215	14	5	7	2						
220	11		10	1						
225	13		10	3						
230	29		20	9						
235	41	1	17	23						
240	59		20	36	3					
245	31		7	24						
250	41		6	34	1					
255	42		7	33	2					
260	47		1	36	10					
265	45		4	25	16					
270	73			43	30					
275	46		1	28	17					
280	68			28	39	1				
285	47			20	27					
290	34			9	25					
295	39			10	26	1				
300	48			8	37	3				
305	44			11	31	2				
310	25			2	19	4				
315	23				11	12				
320	26			1	16	8	1			
325	25			1	15	8	1			
330	13				3	5	5			
335	9				3	5	1			
340	1						1			
345	2				1	1				
350	2						2			
355										
360	1						1			
365										
370										
375										

TABLE 13. Continued.

mm FL	Total sampled	Age groups								
		0	I	II	III	IV	V	VI	VII	VIII
380										
385	1								1	
390										
395										
400										
405										
410										
415	1									1
Total	942	19	138	387	334	50	12	0	1	1
Mean FL	273	204	231	265	293	320	337	0	386	416

TABLE 14. Length distribution of jack mackerel landed in southern California for 1972 to 1977 seasons. Estimates of the number of fish in thousands by length group.

Length Group	1972 Estimate	1972 Pct	1973 Estimate	1973 Pct	1974 Estimate	1974 Pct	1975 Estimate	1975 Pct	1976 Estimate	1976 Pct	1977 Estimate	1977 Pct
130-139	1060	.9	132	.2							68	.1
140-149	1787	1.5	318	.5					172	.1	124	.1
150-159	1147	1.0	1062	1.8					2595	1.6	674	.5
160-169	791	.7	2677	4.5	406	.7	58	trace	5265	3.2	1854	1.4
170-179	1999	1.7	3221	5.4	1201	2.0	472	.3	4409	2.7	1150	.9
180-189	3359	2.8	5131	8.7	5072	8.5	1098	.6	5810	3.5	1639	1.2
190-199	3670	3.1	4477	7.6	3188	5.3	1854	1.0	4542	2.7	2884	2.1
200-209	8969	7.6	4894	8.3	3062	5.1	6389	3.6	4063	2.5	4471	3.3
210-219	15477	13.1	6277	10.6	3374	5.6	22985	12.9	5444	3.3	4907	3.6
220-229	14662	12.4	6116	10.3	5564	9.3	46576	26.1	5978	3.6	9549	7.1
230-239	12048	10.2	3631	6.1	10923	18.3	37102	20.8	6515	3.9	24188	17.9
240-249	10989	9.3	3813	6.4	11069	18.5	21622	12.1	3652	2.2	25755	19.1
250-259	10154	8.6	2587	4.4	4219	7.1	12340	6.9	4800	2.9	18743	13.9
260-269	11184	9.5	3438	5.8	2834	4.7	8569	4.8	16108	9.7	8536	6.3
270-279	8902	7.5	2850	4.8	2181	3.6	3705	2.1	26415	16.0	6345	4.7
280-289	6674	5.6	1749	2.9	1075	1.8	3772	2.1	25139	15.2	4012	3.0
290-299	2860	2.4	1384	2.3	1500	2.5	4609	2.6	18338	11.1	3793	2.8
300-309	1646	1.4	1621	2.7	1868	3.1	3512	2.0	14005	8.5	5517	4.1
310-319	345	.3	1312	2.2	1180	2.0	1777	1.0	6894	4.2	5192	3.8
320-329	295	.2	1730	2.9	843	1.4	903	.5	3057	1.8	2688	2.0
330-339	84	.1	533	.9	129	.2	664	.4	1384	.8	1491	1.1
340-349	51	trace	298	.5			253	.1	339	.2	886	.7
350-359							153	.1	270	.2	384	.3
360-369							51	trace	69	trace	47	trace
370-379			43	.1			101	.1	127	.1	44	trace
380-389					74	.1	101	.1				
390-399									69	trace		
400-409												
410-419												
420-429									35	trace	47	trace
430-439												
440-449												
450+									69	trace		

TABLE 15. Length distribution of jack mackerel landed in southern California for 1978 to 1983 seasons. Estimates of the number of fish in thousands by length group.

Length group	1978 Estimate	1978 Pct	1979 Estimate	1979 Pct	1980 Estimate	1980 Pct	1981 Estimate	1981 Pct	1982 Estimate	1982 Pct	1983 Estimate	1983 Pct
130-139			53	.1								
140-149			58	.1	53	trace	37	trace				
150-159	175	.1	618	.7	469	.4	148	.1				
160-169	233	.2	646	.7	2314	2.0	37	trace				
170-179	1146	.9	709	.7	7746	6.6	188	.2	109	.1	25	.1
180-189	2434	2.0	1142	1.2	13763	11.8	1339	1.2	188	.2	108	.4
190-199	4225	3.5	1539	1.6	11530	9.9	1480	1.4	187	.2	252	.9
200-209	3608	3.0	2203	2.3	5395	4.6	2269	2.1	349	.3	420	1.5
210-219	5047	4.1	3447	3.6	2811	2.4	8401	7.8	1771	1.5	548	2.0
220-229	6391	5.2	8154	8.6	1930	1.7	10753	10.0	2467	2.1	764	2.8
230-239	9029	7.4	16754	17.7	1881	1.6	16701	15.5	3882	3.2	2324	8.4
240-249	7809	6.4	25515	26.9	4249	3.6	21389	19.9	12983	10.9	2720	9.9
250-259	9827	8.0	14255	15.0	6515	5.6	15931	14.8	29558	24.7	2384	8.6
260-269	15134	12.4	6981	7.4	8165	7.0	9960	9.3	26850	22.5	2990	10.8
270-279	22729	18.6	4764	5.0	9242	7.9	3288	3.1	19835	16.6	3864	14.0
280-289	14966	12.2	2586	2.7	13531	11.6	2319	2.2	11798	9.9	3269	11.9
290-299	7329	6.0	1249	1.3	15327	13.1	3099	2.9	4801	4.0	2119	7.7
300-309	2743	2.2	1406	1.5	6414	5.5	2538	2.4	2298	1.9	2521	9.1
310-319	2131	1.7	976	1.0	2021	1.7	2386	2.2	687	.6	1224	4.4
320-329	2232	1.8	802	.8	785	.7	2246	2.1	503	.4	1310	4.8
330-339	1989	1.6	494	.5	205	.2	1292	1.2	682	.6	559	2.0
340-349	1529	1.3	305	.3	438	.4	695	.6	208	.2	63	.2
350-359	886	.7	163	.2	559	.5	212	.2	155	.1	53	.2
360-369	406	.3	72	.1	237	.2	269	.3	155	.1	18	.1
370-379	187	.2			218	.2	37	trace				
380-389					427	.4	138	.1	52	trace	18	.1
390-399	44	trace			474	.4	106	.1				
400-409					53	trace	106	.1				
410-419					132	.1	35	trace			18	.1
420-429												
430-439							35	trace				
440-449					53	trace						
450+												

TABLE 16. Age and year class composition of jack mackerel landed in southern California for the 1972-1977 seasons.

Age group	0	I	II	III	IV	V	VI	VII	VIII	IX	
1972-73 Season											
Year class	1972	1971	1970	1969	1968	1967	1966	1965	1964	1963	TOTAL
Thousands of fish	26604	33808	36873	17433	3045	288	102	0	0	0	118153
Percent	22.5	28.6	31.2	14.8	2.6	.2	.1	.0	.0	.0	100.0
Thousands of pounds	4604	9646	15002	9123	1911	241	101	0	0	0	40628
Percent	11.3	23.7	36.9	22.5	4.7	.6	.2	.0	.0	.0	100.0
1973-74 Season											
Year class	1973	1972	1971	1970	1969	1968	1967	1966	1965	1964	TOTAL
Thousands of fish	17384	18330	11235	6209	2845	2203	1005	85	0	0	59296
Percent	29.3	30.9	18.9	10.5	4.8	3.7	1.7	.1	.0	.0	100.0
Thousands of pounds	2500	4659	4240	3390	2113	1859	907	80	0	0	19748
Percent	12.7	23.6	21.5	17.2	10.7	9.4	4.6	.4	.0	.0	100.0
1974-75 Season											
Year class	1974	1973	1972	1971	1970	1969	1968	1967	1966	1965	TOTAL
Thousands of fish	12762	9623	24291	6955	4156	1718	203	55	0	0	59763
Percent	21.4	16.1	40.6	11.6	7.0	2.9	.3	.1	.0	.0	100.0
Thousands of pounds	1959	2657	8178	3223	2846	1388	195	53	0	0	20499
Percent	9.6	13.0	39.9	15.7	13.9	6.8	1.0	.3	.0	.0	100.0
1975-76 Season											
Year class	1975	1974	1973	1972	1971	1970	1969	1968	1967	1966	TOTAL
Thousands of fish	0	132469	25752	10188	7857	1793	354	202	51	0	178666
Percent	.0	74.1	14.4	5.7	4.4	1.0	.2	.1	0.0	.0	100.0
Thousands of pounds	0	35484	9980	5551	5253	1473	396	244	74	0	58455
Percent	.0	60.7	17.1	9.5	9.0	2.5	.7	.4	.1	.0	100.0
1976-77 Season											
Year class	1976	1975	1974	1973	1972	1971	1970	1969	1968	1967	TOTAL
Thousands of fish	35276	20309	101160	8006	607	139	0	0	69	0	165566
Percent	21.3	12.3	61.1	4.8	.4	.1	.0	.0	0.0	.0	100.0
Thousands of pounds	5966	8068	59287	5593	704	187	0	0	177	0	79982
Percent	7.5	10.1	74.1	7.0	.9	.2	.0	.0	.2	.0	100.0
1977-78 Season											
Year class	1977	1976	1975	1974	1973	1972	1971	1970	1969	1968	TOTAL
Thousands of fish	11767	94044	14883	12695	1396	156	47	0	0	0	134988
Percent	8.7	69.7	11.0	9.4	1.0	.1	0.0	.0	.0	.0	100.0
Thousands of pounds	2171	31750	8205	9791	1282	167	95	0	0	0	53461
Percent	4.1	59.4	15.3	18.3	2.4	.3	.2	.0	.0	.0	100.0

TABLE 17. Age and year class composition of jack mackerel landed in southern California for the 1978-1983 seasons.

Age group	0	I	II	III	IV	V	VI	VII	VIII	IX	
1978-79 Season											
Year class	1978	1977	1976	1975	1974	1973	1972	1971	1970	1969	Total
Thousands of fish	21689	27146	59590	8183	3895	1610	115	0	0	0	122228
Percent	17.7	22.2	48.8	6.7	3.2	1.3	.1	.0	.0	.0	100.0
Thousands of pounds	4924	10165	32576	6102	3750	1890	130	0	0	0	59537
Percent	8.3	17.1	54.7	10.2	6.3	3.2	.2	.0	.0	.0	100.0
1979-80 Season											
Year class	1979	1978	1977	1976	1975	1974	1973	1972	1971	1970	Total
Thousands of fish	10251	72053	8072	3250	654	611	0	0	0	0	94891
Percent	10.8	75.9	8.5	3.4	.7	.6	.0	.0	.0	.0	100.0
Thousands of pounds	2336	25337	3935	2357	627	638	0	0	0	0	35230
Percent	6.6	71.9	11.2	6.7	1.8	1.8	.0	.0	.0	.0	100.0
1980-81 Season											
Year class	1980	1979	1978	1977	1976	1975	1974	1973	1972	1971	Total
Thousands of fish	43884	18989	47911	3148	1494	901	343	265	0	0	116935
Percent	37.5	16.2	41.0	2.7	1.3	.8	.3	.2	.0	.0	100.0
Thousands of pounds	6732	7421	27834	2230	1565	1221	539	498	0	0	48040
Percent	14.0	15.4	57.9	4.6	3.3	2.5	1.1	1.0	.0	.0	100.0
1981-82 Season											
Year class	1981	1980	1979	1978	1977	1976	1975	1974	1973	1972	Total
Thousands of fish	3698	83677	9922	7690	1822	519	71	35	0	0	107434
Percent	3.4	77.9	9.2	7.2	1.7	.5	.1	0.0	.0	.0	100.0
Thousands of pounds	586	28427	5174	5837	1716	671	119	62	0	0	42592
Percent	1.4	66.7	12.1	13.7	4.0	1.6	.3	.1	.0	.0	100.0
1982-83 Season											
Year class	1982	1981	1980	1979	1978	1977	1976	1975	1974	1973	Total
Thousands of fish	1616	10140	98608	7427	1144	455	128	0	0	0	119518
Percent	1.4	8.5	82.5	6.2	1.0	.4	.1	.0	.0	.0	100.0
Thousands of pounds	371	3303	43453	4249	1071	478	125	0	0	0	53050
Percent	.7	6.2	81.9	8.0	2.0	.9	.2	.0	.0	.0	100.0
1983-84 Season											
Year class	1983	1982	1981	1980	1979	1978	1977	1976	1975	1974	Total
Thousands of fish	480	4029	11259	10147	1336	282	0	18	0	18	27569
Percent	1.7	14.6	40.8	36.8	4.8	1.0	.0	.1	.0	.1	100.0
Thousands of pounds	117	1249	5044	6015	1009	252	0	21	0	29	13736
Percent	.9	9.1	36.7	43.8	7.3	1.8	.0	.2	.0	.2	100.0

TABLE 18. Numbers of jack mackerel landed in thousands by age group for each year-class from the 1947 through 1983 seasons. Data include all southern California landings for all years.

Year-Class	Age of fish 0	I	II	III	IV	V	VI	VII	VIII	Total
1939	--	--	--	--	--	--	--	--	274	274
1940	--	--	--	--	--	--	--	687	240	927
1941	--	--	--	--	--	--	2759	362	15	3136
1942	--	--	--	--	--	18861	947	562	1402	21772
1943	--	--	--	--	51104	1789	2400	4542	14	59849
1944	--	--	--	104842	15407	6674	11968	441	1987	141319
1945	--	--	61435	34018	19788	12654	2054	7398	0	137347
1946	--	9434	24691	43568	15942	6139	29737	0	0	129511
1947	5835	26091	83556	102485	45379	33372	0	0	0	296718
1948	0	1601	14837	24984	20446	0	0	0	0	61868
1949	159	3329	20309	39088	0	0	0	1166	1009	65060
1950	1595	13902	20664	28	0	169	4180	3510	0	44048
1951	321	8877	2259	1954	9225	17861	6080	13	0	46590
1952	121176	30137	16851	65289	46741	9062	76	0	0	289332
1953	30931	20516	28255	33839	6514	293	1248	0	0	121596
1954	133	41735	28223	4841	2139	2136	0	0	0	79207
1955	850	50089	5816	5841	6601	156	285	0	0	69638
1956	13720	7102	15860	10414	2764	636	171	30	0	50697
1957	1159	26566	32930	32085	13355	1995	142	205	0	108437
1958	83780	123615	106246	68367	13249	3900	1844	0	53	401054
1959	1623	21773	89978	100219	31016	2728	312	45	0	247694
1960	15269	92211	65515	76822	18644	1191	143	0	0	269795
1961	7872	36153	48036	43066	6933	697	58	0	0	142815
1962	1658	17964	59613	16560	3620	0	106	0	0	99521
1963	19352	46719	40860	11668	65	799	0	0	0	119463
1964	30511	98845	24458	1008	2331	102	61	0	0	157316
1965	84943	34513	9719	13410	2521	741	0	0	0	145847
1966	95242	31642	75129	9125	4307	92	102	85	0	215724
1967	192957	116629	28452	10133	398	288	1005	55	51	349968
1968	78895	151103	20879	4725	3045	2203	203	202	69	261324
1969	30931	102232	39493	17433	2845	1718	354	0	0	195006
1970	125376	171400	36873	6209	4156	1793	0	0	0	345807
1971	22690	33808	11235	6955	7857	139	47	0	0	82731
1972	26604	18330	24291	10188	607	156	115	0	0	80291
1973	17384	9623	25752	8006	1396	1610	0	265	0	64036
1974	12762	132469	101160	12695	3895	611	343	35	18	263988
1975	0	20309	14883	8183	654	901	71	0	0	45001
1976	35276	94044	59590	3250	1494	519	128	18	--	194319
1977	11767	27146	8072	3148	1822	455	0	--	--	52410
1978	21689	72053	47911	7690	1144	282	--	--	--	150769
1979	10251	18989	9922	7427	1336	--	--	--	--	47925
1980	43884	83677	98608	10147	--	--	--	--	--	236316
1981	3698	10140	11259	--	--	--	--	--	--	25097
1982	1616	4029	--	--	--	--	--	--	--	5645
1983	480	--	--	--	--	--	--	--	--	480
Total	1152389	1808795	1413620	959710	368740	132722	66939	19621	5132	5927668

TABLE 19. Pounds of jack mackerel landed in thousands by age group for each year-class from the 1947 through 1983 season landings. Include all southern California landings for all years.

Year-class	Age of fish caught 0	I	II	III	IV	V	VI	VII	VIII	Total
1939	--	--	--	--	--	--	--	--	414	414
1940	--	--	--	--	--	--	--	863	234	1097
1941	--	--	--	--	--	--	3030	313	24	3367
1942	--	--	--	--	--	17867	876	684	1947	21374
1943	--	--	--	--	38744	1780	2693	5963	14	49194
1944	--	--	--	57397	11261	6393	13897	441	3391	92780
1945	--	--	21461	19117	14615	12326	2054	11082	0	80655
1946	--	1583	8946	22722	11995	6139	36249	0	0	87634
1947	641	5807	32221	52215	45379	31734	0	0	0	167997
1948	0	387	5557	24984	16235	0	0	0	0	47163
1949	21	931	20309	24712	0	0	0	1134	987	48094
1950	316	13902	10003	18	0	123	3721	3666	0	31749
1951	321	2716	1055	1018	5340	18769	6043	18	0	35280
1952	20490	10247	6720	31961	31082	7867	92	0	0	108459
1953	4918	6283	11276	18262	4481	266	1188	0	0	46674
1954	24	10891	10728	2533	1353	1766	0	0	0	27295
1955	132	12286	2136	2892	4430	109	240	0	0	22225
1956	1822	1418	5374	5210	1926	541	170	45	0	16506
1957	130	5785	11792	15845	8826	5945	141	279	0	48743
1958	10168	26307	39190	36338	9862	3362	1901	0	79	127207
1959	219	5421	32523	49822	21301	2381	299	55	0	112021
1960	2158	23379	20835	40804	12677	980	156	0	0	100989
1961	1059	6123	17721	22710	4809	536	51	0	0	53009
1962	163	3826	21690	7943	2323	0	93	0	0	36038
1963	2373	11328	13121	5751	52	686	0	0	0	33311
1964	3837	23855	9527	521	1546	113	69	0	0	39468
1965	11437	9460	3420	6761	1573	721	0	0	0	33372
1966	13265	6926	11317	5010	3187	144	101	80	0	40030
1967	25555	28031	9334	5581	314	241	907	53	74	70090
1968	10278	16110	8128	2335	1911	1859	195	244	177	41237
1969	4648	22573	13166	9123	2113	1388	396	0	0	53407
1970	16772	36429	15002	3390	2846	1473	0	0	0	75912
1971	3819	9646	4240	3223	5253	187	95	0	0	26463
1972	4604	4659	8178	5551	704	167	130	0	0	23993
1973	2500	2657	9980	5593	1282	1890	0	498	0	24400
1974	1959	35484	59287	9791	3750	638	539	62	29	111539
1975	0	8068	8205	6102	627	1221	119	0	0	24342
1976	5966	31750	32576	2357	1565	671	125	21	--	75031
1977	2171	10165	3935	2230	1716	478	0	--	--	20695
1978	4924	25337	27834	5837	1071	252	--	--	--	65255
1979	2336	7421	5174	4249	1009	--	--	--	--	20189
1980	6732	28427	43453	6015	--	--	--	--	--	84627
1981	586	3303	5044	--	--	--	--	--	--	8933
1982	371	1249	--	--	--	--	--	--	--	1620
1983	117	--	--	--	--	--	--	--	--	117
Totals	166832	460170	570458	525923	277158	131013	75570	25501	7370	2239995

8942

Reanalysis of Recruitment Estimates of the Peruvian Anchoveta in Relationship to Other Population Parameters and the Surrounding Environment

ROY MENDELSSOHN
Pacific Fisheries Environmental Group
Southwest Fisheries Center
National Marine Fisheries Service, NOAA
P.O. Box 831, Monterey
California 93942 USA

MENDELSSOHN, R. 1989. A reanalysis of recruitment estimates of the Peruvian anchoveta in relationship to other population parameters and the surrounding environment, p. 364-385. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Abstract

New recruitment estimates of the Peruvian anchoveta are analysed with respect to other population parameters and the surrounding ocean environment. The inshore and offshore environmental variables differ in their dynamics, and the inshore series vary north to south. For the inshore locations, it is not possible to resolve if a wind-related effect is due to transport or turbulence. The new recruitment estimates differ significantly from the old estimates, partly due to mackerel consumption acting as a surrogate for SST. Models using the monthly data were not possible due to correlations in the populations that could be spurious. On a yearly basis, a nonlinear additive model using parent biomass and transport at Trujillo explained 75% of the variance in the recruitment estimates.

Resumen

Nuevos estimados de reclutamiento de la anchoveta peruana se analizan en relación con otros parámetros poblacionales y el ambiente en que habita. Las variables ambientales costeras y distantes de la costa difieren en su dinámica, y las series costeras varian de norte a sur. Para las localidades costeras, no es posible establecer si un efecto relacionado con el viento es ocasionado por el transporte o la turbulencia. Los nuevos estimados de reclutamiento difieren significativamente de los estimados antiguos, debido parcialmente al consumo del jurel que actúa como un indicador de la temperatura. No ha sido posible aplicar modelos que utilizan datos mensuales debido a que las correlaciones en la población pudieran ser espurias. Un modelo aditivo no lineal usando la biomasa parental y el transporte de Trujillo, sobre una base anual, explica el 75% de la variancia de los estimados del reclutamiento.

Introduction

One of the main goals of the contributions in Pauly and Tsukayama (1987) was to estimate the demographic parameters of the Peruvian anchoveta, taking into account all sources of mortality. Thus, estimates of anchoveta consumption by birds (Muck and Pauly 1987), marine mammals (Muck and Fuentes 1987) and bonito (Pauly et al. 1987) were included in the estimation algorithms. Muck and Sanchez (1987), however, presented evidence that mackerel and horse mackerel are major predators of the anchoveta, with consumptions levels approaching that of the fishery at its highest levels. As the mackerel consumption was not included in the original estimates, new population estimates have been calculated (Pauly and Palomares, this vol.).

These new population estimates, as well as the corrected alongshore stress series in Bakun and Mendelssohn (this vol.), are the impetus for redoing the analysis in Mendelssohn and Mendo (1987, hereafter referred to as M&M). Besides examining some models for using population and environmental parameters to forecast the new estimates of anchoveta recruitment, this reanalysis affords me the opportunity to delve in more detail into some issues glossed over in M&M, as well as to tie together some loose ends. In particular, the interrelationships among some environmental variables mentioned in M&M are discussed here in more detail.

M&M used a form of non-parametric regression that estimated transformations for both the dependent and the independent variables. The algorithm did not produce tables analogous to the ANOVA tables in linear regression. Non-parametric regressions are also used in this paper, but in a form more analogous to standard regression analysis, even allowing "error bars" on the estimated transformations. This should make the resulting models more easily interpreted. Cury and Roy (1989) estimate optimal environmental windows for a number of eastern boundary current regions, including the Peruvian anchoveta. I reestimate these windows for the new data. Finally, Bohle-Carbonell (this vol.) examines fractal dimensions for some of the time series in Pauly and Tsukayama (1987). I estimate a related parameter, fractional differencing, for a larger number of the environmental series, and show how these estimates relate to the models of this paper.

Many of these issues were examined in my original efforts with Jaime Mendo, but were only alluded to in M&M. My knowledge of the Peruvian ecosystem derives from my working with J. Mendo, and while we did not work on this reanalysis together, I would like to acknowledge my debt to him and indicate that this paper would not have been possible otherwise.

Data and Methods

For the population data, I use the estimates of recruitment, parent and female biomass, and egg production in Pauly and Palomares (this vol.) and Pauly and Soriano (this vol.). For the environmental series, I use the corrected alongshore stress given in Bakun and Mendelssohn (this vol.), the turbulence series ("wind speed cubed") in Bakun (1987), the Southern Oscillation Index (SOI) in Brainard and McLain (1987), and the estimates of upwelling and turbulence for Trujillo and Callao in Mendo et al. (1987). For convenience, I will refer to the Bakun estimates of transport and turbulence as the "oceanic" estimates, while the estimates of Mendo et al. (1987) will be referred to by location.

Spectral estimates were calculated for the mean corrected series by first tapering the series using a split-cosine bell taper (Bloomfield 1976)

$$u_t = \begin{cases} .5\left(1-\cos\left(\pi\left(t-.5\right)/m\right)\right), & t=0, \ldots, m-1 \\ 1, & t=m, \ldots, n-m-1 \\ .5\left(1-\cos\left(\pi\left(n-t+.5\right)/m\right)\right), & t=n-m, \ldots, n-1, \end{cases} \qquad \ldots 1)$$

where m is chosen so that 2m/n is the desired proportion of the data to be tapered. I have used a 20% taper. Tapering data reduces leakage between frequencies, but tends to make spectral peaks flatter and broader. The discrete Fourier transform of each tapered series was calculated as

$$d_x(\lambda_j) = \frac{1}{T}\sum_{t=0}^{T-1} e^{-i\lambda_j t} x(t) \qquad \ldots 2)$$

where $\lambda_j = (2\pi j)/T$ is the j th Fourier frequency. The raw (cross)-periodogram is then calculated as

$$p_{xy}(\lambda_j) = d_x(\lambda_j) d^*_y(\lambda_j) \qquad \ldots 3)$$

where the notation d^* denotes conjugate (transpose). Spectral density matrices were then calculated as the overlapping moving average of the raw periodograms,

$$f_{xy}(\lambda_j) = \sum_{l=-m}^{m} p_{xy}(\lambda_{j+l}). \qquad \text{... 4)}$$

I have used a value of $m = 5$, giving 22 degrees of freedom.

Most analyses of time series data assume stationarity, or that stationarity can be achieved after applying a relatively short-term filter to the data. This assumption may not be valid for natural processes. Hurst (1951) studied the flows of rivers. Let $x_1, x_2, \ldots, x_T$ be the historical sequence of flows. Then the cumulative flows up to time t are

$$Su_t = \sum_{j=1}^{t} x_j, \quad t = 1, 2, \ldots, T. \qquad \text{... 5)}$$

Related to reservoir construction is the sequential range

$$R = \max Su_t - \min Su_t \qquad \text{... 6)}$$

Hurst (1951) looked at the normalized sequential range (or "rescaled adjusted range") where Su_t has the mean flow removed and the result is divided by the standard deviation of the flows. If the flows are independent over long time scales, then one would expect that $R/S \sim (T/2)^{.5}$. However, Hurst (1951) found that for a wide range of river flows $R/S \sim (T/2)^H$ for H in the range (.6,.8). This can be explained in terms of fractional Gaussian noise (fGn) (Mandelbrot and Van Ness 1968, Mandelbrot 1971). Let $B(s)$ be Brownian motion, a stochastic process such that $B(s+u)-B(s)$ are $N(0,1)$ and independent. Then fractional Brownian motion takes the form

$$B_H(t) = \int_{-\infty}^{t} (t-a)^{H-.5}\, dB(s), \quad -\infty < t < \infty \qquad \text{... 7)}$$

or

$$B_H(t) - B_H(0) = \int_{-\infty}^{t} (t-s)^{H-.5}\, dB(s) - \int_{-\infty}^{0} (-s)^{H-.5}\, dB(s). \qquad \text{... 8)}$$

Discretizing the equation yields

$$b_t(H) = B_H(t) - B_H(t-1). \qquad \text{... 9)}$$

Fractional Gaussian noise can be described by its autocorrelation function

$$C(s) = \frac{1}{2}(\,|s-1|^{2H} - 2|s|^{2H} + |s+1|^{2H}\,). \qquad \text{... 10)}$$

Fractional Gaussian noise also exhibits the self-similarity property, that is

$$x(t\lambda) \sim (\lambda)^{a} x(t). \qquad \text{... 11)}$$

A concept related to *fGn* is "fractional differencing" (Granger and Joyeux 1980, Hosking 1981) described as

$$(1-B)^{d} x(t) = e(t) \qquad \text{... 12)}$$

where d is possibly nonintegral, B is the backshift operator, and the $e(t)$ are independently distributed as $N(0, \sigma^2)$. Note that this is not a nonintegral lag operator, but rather an infinitely lagged polynomial in B whose weights die out at a rate given in the autoregressive representation (14). The spectral density of this model is

$$f(\lambda) = \frac{\sigma^2}{2\pi}(2(1-\cos(\lambda)))^{-d}, \quad \lambda \neq 0. \qquad \text{... 13)}$$

Granger and Joyeux (1980) derive the following autoregressive representation of a fractionally differenced process

$$\sum a_j x(t-j) = e(t); \qquad a_j = \frac{\Gamma(j-d)}{\Gamma(1-d)\Gamma(j+1)} \quad j > 1. \qquad \text{... 14)}$$

Porter-Hudak (1982) and Geweke and Porter-Hudak (1983) show that the power spectrums of the error terms from an *fGn* process and a fractionally differenced process only differ by a short-term memory component. Thus both models are estimating essentially the same long-term memory component. I find fractional differencing more intuitive, as it is a long-term extension of the usual ideas of differencing and filtering to obtain stationarity. (The first few terms of the expansion of the differencing polynomial are

$$1 - dB - \frac{1}{2}d(1-d)B^2 - \frac{1}{6}d(1-d)(2-d)B^3 \qquad \text{... 15)}$$

The parallels with the usual differencing schemes used to achieve stationarity are immediate.)

Porter-Hudak (1982) and Kashyap and Eom (1988) give methods for estimating the fractional differencing parameter *d*, based on regressions between the log of the theoretical spectrum and the log of the observed periodogram. The property of concern here is that a process has long-term memory if d is in the range $(0,.5)$; the process has short-term memory if $d < 0$; and the process has infinite variance if $d > .5$ (Granger and Joyeux 1980, Hosking 1981). Both long-term and short-term memory time series models assume that the basic input process is a random variable. The main difference is that in long-memory models any impulse to the system takes a long time to die out. Another way to view this is that the system is sensitive to initial conditions. A small difference in two identical systems at a given time period will be evident for many time periods to come. Depending on the dynamics involved, the difference between the two systems caused by this impulse may grow, rather than disappear through time. The models in M&M as well as the ones in this paper, assume a relationship between anchoveta recruitment and other variables. If this relationship is on the proper scale and is stationary, then long-term memory in any of the predictor variables will not affect the system. However, the length of time ahead that a forecast can be made can be affected by long-term memory, as longer forecast horizons could imply forecasting one of the predictor variables. As errors can propogate in long-memory systems, long-term predictions become unreliable. An alternative is to find another, less direct predictor variable, that is related to anchoveta recruitment at a longer lag. (See also Bohle-Carbonell, this vol., who estimates the fractal dimension of several of the series in Pauly and Tsukayama 1987).

Trends in time-series are estimated using two different algorithms. The first is the "locally-weighted sums of squares" or LOWESS algorithm of Cleveland (1979), and the other is the decomposition algorithm of Kitagawa and Gersch (1984). LOWESS fits to each point a weighted linear regression using some fixed percentage of points surrounding the given point. The regression is then made robust by weighting against outliers. I use a proportion of $F = .05$, which corresponds to two years of data in calculating the smooths in this paper.

Kitagawa and Gersch (1984) assume that an observed time series can be decomposed as

$$y(t) = T(t) + S(t) + A(t) + e(t) \qquad \text{... 16)}$$

where $T(t)$ is a trend component at time t, $s(t)$ is a seasonal component at time t, $A(t)$ is a stationary random component (i.e., and AR component) at time t, and $e(t)$ is an error term. They assume a smoothness prior for the trend and seasonal components, which means that at some level of differencing the component is equivalent to a zero mean normal variate with unknown variance. The degree of differencing and the amount of variance in the random variate causes a tradeoff between the smoothness of the component and the reduction in variance due to that component. This is the same as fitting the discrete equivalent of a smoothing spline for that component (Kohn and Ansley 1988). Kitagawa and Gersch (1984) show that this can be formulated as a state-space model and estimated using a combination of Kalman filtering and maximum likelihood estimation.

The usual regression model has a response random variable Y and p predictor random variables $X_1, X_2, \ldots, X_p$. A set of n independent realizations of these random variables is observed, denoted by $(y_1, x_{11}, \ldots, x_{1p}), \ldots, (y_n, x_{n1}, \ldots, x_{np})$ and it is desired to estimate the conditional expectation $E(Y \mid X_1, X_2, \ldots, X_p)$. Linear regression assumes that the conditional expectation is linear, that is

$$E(Y \mid X_1, X_2, \ldots, X_p) = \beta_0 + \beta_1 X_1 + \ldots + \beta_p X_p, \qquad \ldots 17)$$

and given a sample, estimates of the β_i are usually found by least squares. A natural generalization is to consider additive nonlinear models (Hastie and Tibshirani 1986) of the form

$$E(Y \mid X_1, X_2, \ldots, X_p) = \sum_{j=1}^{p} s_j(X_j) \qquad \ldots 18)$$

where the nonlinear functions s_j are to be estimated. This is accomplished by estimating the s_j as an "average" of some part of the data surrounding a point, in this case a scatterplot smoother fit using the backfitting algorithm of Breiman and Friedman (1985). In particular, I use the running lines smoother in Hastie and Tibshirani (1986).

When the functions s_j in generalized additive models are estimated using a fixed span smoother, then it is possible to estimate the degrees of freedom used in forming the estimate of s_j, as well as an analysis of deviance table that is directly analogous to the standard analysis of variance table in regression analysis (Hastie and Tibshirani 1986; see Hastie 1987 for a good description of deviance and how it relates to sums of squares). This allows for a comparison of models using measures such as AIC (Akaike 1977), BIC (Schwarz 1978) or cross-validation. A smaller span produces a closer fit to the observed data (smaller variance), but with a greater bias and larger number of degrees of freedom, equivalent to fitting more parameters in a normal regression model. A larger span is smoother, with smaller bias, but greater variance. The choice of the span is thus a tradeoff between variance and bias, as in most situations where extra parameters can be added to the model. Hastie and Tibshirani (1985) show how to construct 95% confidence intervals for the estimated functions s_j.

Environmental Variables

There are a large number of environmental variables that could be used to model the anchoveta, but brute force searching through all of them can lead to spurious results. The environmental variables available for this study in all likelihood are surrogates for the actual physical processes that affect the anchoveta. It is likely, then, that the dynamics of the variables will be the important element in modeling. While each of these large number of series could be argued to be a surrogate variable, it is possible to separate variables that reflect more direct influences on the fish from those with indirect influences. For this reason, the SOI is not used in any of the direct analyses. The SOI reflects processes distant from the environment of the Peruvian anchoveta. The changes reflected in SOI would have to be reflected in changes in the more local environment to have any effect on the anchoveta. If, however, a local variable is a good predictor of anchoveta recruitment, and there is a strong relationship between the SOI and this local variable, then there exists the possibility for a more extended (longer lead time) forecast.

For completeness, I show the major environmental series with trends estimated using LOWESS. SST (Fig. 1), shows a sharp drop through 1954-1956, and then a peak during the El Niño period of 1957-58. SST remained fairly steady through mid-1971, and then peaked in the 1972 El Niño. The 1983 El Niño produced a strong peak in the series. A slight upward trend in SST is noticeable from 1971 onward.

Oceanic transport (Fig. 2) has been fairly steady, with noticeable increases during the El Niño periods of 1957-58, 1972 and 1983. The 1960s appeared to have been a decade of decreased variance in the transport, and the mean level during the 70s and 80s appears to be somewhat higher.

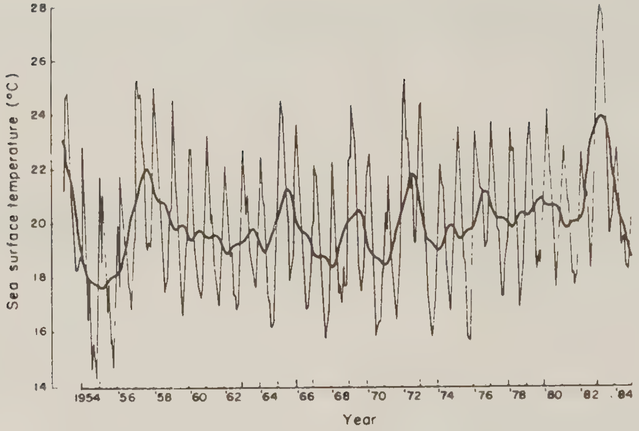


Fig. 1. SST off Peru with estimated local trend line.
Fig. 1. TSM frente a Perú con línea de la tendencia local estimada.

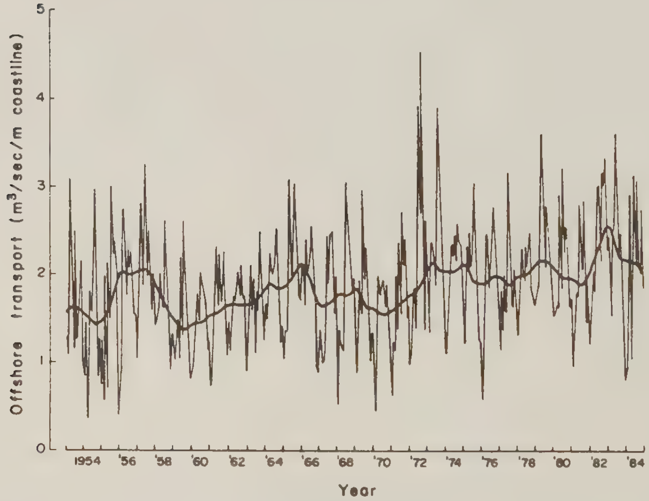


Fig. 2. Oceanic transport off Peru with estimated local trend line.
Fig. 2. Transporte oceánico frente a Perú con línea de la tendencia local estimada.

Transport at Trujillo (Fig. 3) shows the strongest trends among the data series. Transport increased through the El Niño of 1958, and then decreased and stayed relatively constant through the early 1960s. Starting around 1968, transport at Trujillo increased, staying at a higher level through 1972. Transport then dropped sharply till 1974, rose again till 1976, and then declined very sharply until 1982. Coincindent with the El Niño of 1983, transport at Trujillo increased to a more normal level. Transport at Callao (Fig. 3) displays similar behavior, except that the drop in 1974 is not as precipitous, and the sharp decline from 1976-1983 is not noticeable.

None of the subsurface series in Brainard and McLain (1987) are used in this paper, even though Bohle-Carbonell (this vol.) suggests that the subsurface has the strongest relationship with the earlier recruitment estimates. I note that, as mentioned in the article, only 20% of the subsurface data are from actual observations; the rest are from an interpolation scheme of unknown statistical properties. It would be difficult to ascertain to what degree any fit using these data was due to the actual physical process or due to the interpolator.

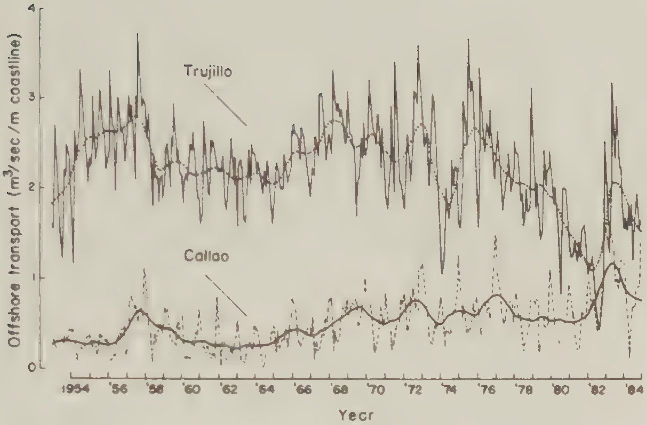


Fig. 3. Transport at Trujillo and Callao, with estimated local trend lines.
Fig. 3. Transporte en Trujillo y Callao, con lineas de las tendencias locales estimadas.

SST also is not used as a predictor. There are good *a priori* reasons for believing that SST would influence anchoveta recruitment. Unfortunately, several of the estimates of anchoveta consumption by other species (Muck and Pauly 1987; Pauly et al. 1987; Muck and Sanchez 1987) make explicit use of SST to modify the amount consumed. In the model of Muck and Sanchez (1987) for mackerel and horse mackerel, the offshore biomass of these fish are assumed at equilibrium sizes, but the relative number of mackerel close to shore varies with SST. Estimated consumption by these species are thus proxy variables for SST. Using SST in any further analysis leads to an obvious, direct bias. SST is also correlated with many of the other environmental variables, which may lead to indirect biases which cannot be totally avoided.

If the environmental variables are viewed as surrogates for a physical process in the ocean, one method for selecting which environmental variables to use in modeling is to see what unique information (in the statistical sense) each of the series contains. If each of the series contains essentially the same information, then there is little matter which is used. If the variables differ greatly in the information contained, then variables should be selected a priori based on knowledge of the fish and of the oceanographic processes likely to affect them.

Bakun and Parrish (1982) and Parrish et al. (1984) give cogent arguments as to why wind-induced transport should be an important factor in recruitment. Lasker (1978) has argued that turbulence affects early survival of larvae by affecting the concentration of available food. Based on these arguments, the transport and turbulence indexes discussed above are natural starting points for the analysis. The SOI will also be examined in relationship to these variables to see if it is reflected in any of these series.

Bakun's estimate of transport and wind is based on averaging a broad area off the coast of Peru, and is dominated by offshore observations. The series of Mendo et al. (1987) are from airports by the coast in Trujillo and Callao, and these authors present anecdotal evidence that these series accurately reflect the nearshore surface winds over the water. If these series differ in their information, then a basis for choosing a series is which area (nearshore or offshore, north or south) most likely influences the areas where the anchoveta are spawning.

The oceanic transport has the expected red noise spectrum at low frequencies, with a strong peak at a yearly frequency and small peaks at the harmonics of the yearly frequency (Fig. 4). Transport at Trujillo and Callao have a weak seasonal signal, and are dominated by the red noise spectrum (Fig. 4). The coherences between the oceanic transport and the transport at Trujillo and Callao are relatively low except at a few frequencies (Fig. 4) and the series are significantly out of phase. This implies that the inshore measures of wind and the oceanic measures contain quite different information about the environment.

Similarly, transport at Trujillo has significantly different dynamics than transport at Callao (Fig. 5). The spectrum of Trujillo transport has a more dominant red noise component, while the

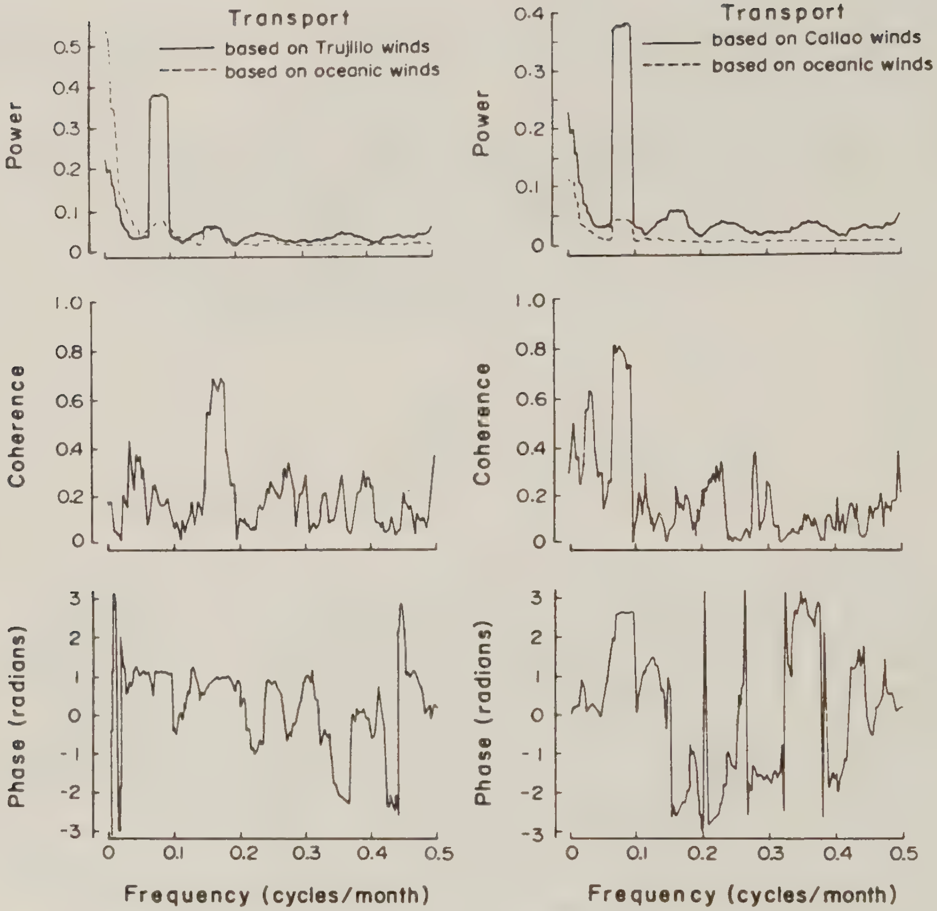


Fig. 4. Spectral analysis of transport off Peru (oceanic winds), Trujillo and Callao (local winds) transport.
Fig. 4. Análisis espectral del transporte frente a Perú (vientos oceánicos), transporte de Trujillo y Callao (vientos locales).

Callao transport has a relatively stronger seasonal cycle. The coherences are not particulary large, and the two series are significantly out of phase. A similar result is valid for the turbulence index at Trujillo and Callao (not shown). Thus, none of the three transport series closely reflects what is occurring in the other two series.

The SOI and oceanic transport have similar spectra, particularly at the yearly frequency and at a peak that would correspond roughly to the occurrence of El Niño (Fig. 5). The two series are highly coherent at these frequencies, and almost 180° out of phase. The same is not true of the SOI and Trujillo transport (Fig. 6), where the main coherence is at the half-yearly frequency. The SOI appears to be a significant advance indicator of what will happen offshore at the longer frequencies, but not of the more inshore behavior.

Long-term memory, if it exists in the ocean, has implications for forecasting too far ahead any process that depends on variables that exhibit this property. The more oceanic series, such as SOI and transport and turbulence calculated over the broad area, exhibit a similar, weak degree of long-term memory (Table 1). The more inshore measures exhibit a stronger long-term memory, approaching infinite variance. As I will be arguing that the more inshore environmental series are the most appropriate, the models involved will be using variables of limited predictability.

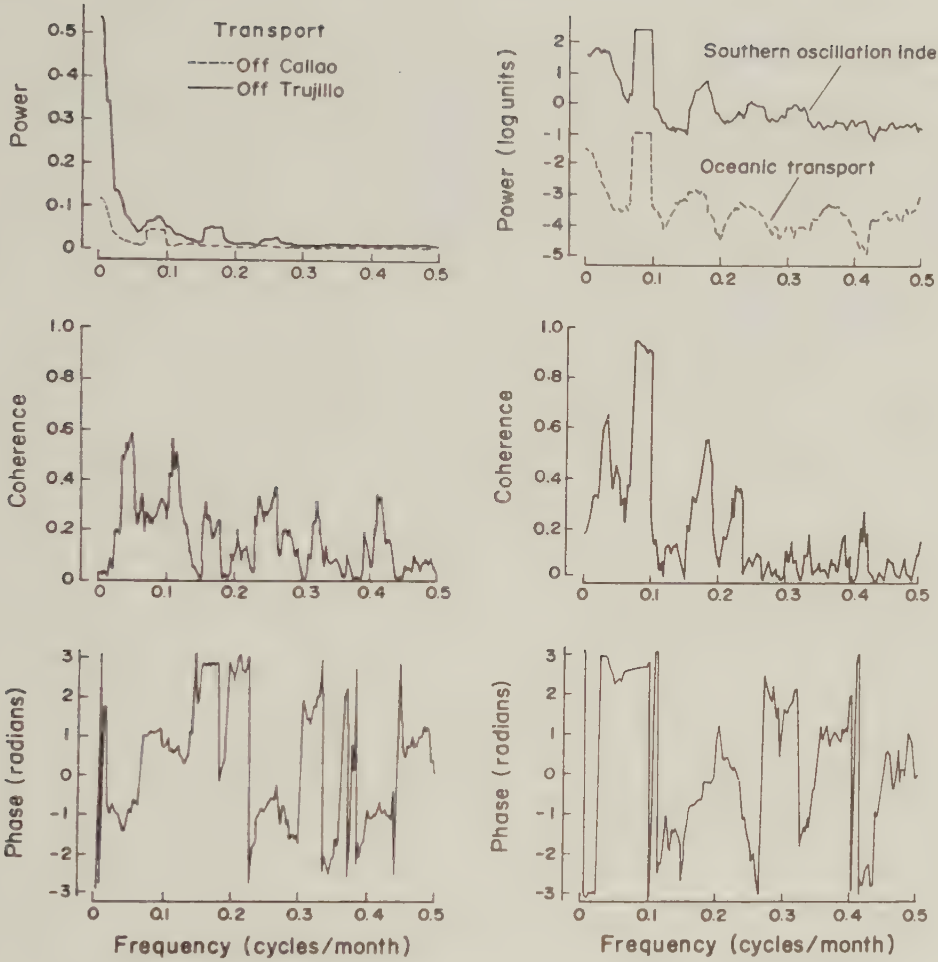


Fig. 5. Spectral analysis of local transport at Trujillo and Callao, of transport off Peru and of SOI.
Fig. 5. Análisis espectral del transporte local en Trujillo y Callao, del transporte frente a Perú y del Indice de Oscilación Sur (SOI).

Turbulence and transport, though both wind-induced, measure very different processes in terms of the anchoveta. If the wind does affect anchoveta recruitment, resolving if it is mainly through transport (most likely transporting larvae offshore) or mainly through turbulence (by affecting food availabilty to larvae) is an important issue. At Trujillo, transport and turbulence are highly coherent except at very high frequencies, and in phase at all frequencies (Fig. 6). As mentioned in M&M, the wind at Trujillo is predominantly from one direction, so that transport is close to wind speed squared, while turbulence is wind speed cubed. The difference in behavior at higher frequencies appears to be one of scale, where turbulence is more variable since it is the cube of the observed speed. As I will be using mostly non-linear techniques to model the data, this difference becomes negligible. (For example, on a log scale, the two series will differ by a multiplicative constant, which can be factored into the parameter on the series. This would not be the case if the wind varied greatly in its direction, so that the alonghore stress differed greatly from the wind speed squared). A similar result was found for Callao. Thus, though biologically there are significant differences between transport and turbulence, statistically for the inshore wind series, it will not be possible to discriminate if an effect is due to transport or turbulence.

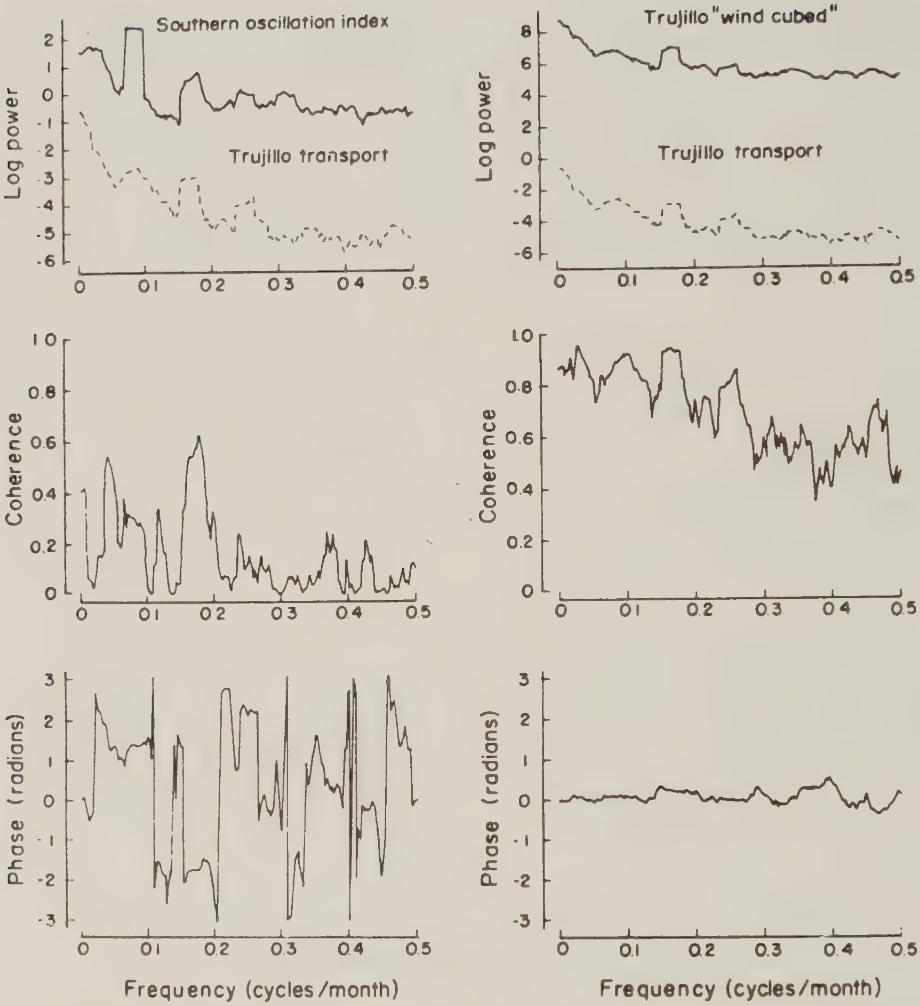


Fig. 6. Spectral analysis of SOI and transport off Trujillo, and of Trujillo transport and turbulence ("wind cubed").
Fig. 6. Análisis espectral del Indice de Oscilación Sur (SOI) y transporte de Trujillo, y del transporte y turbulencia ("viento al cubo") de Trujillo.

Table 1. Estimates of *d*, the fractional differencing parameter, in some environmental series off Peru.
Tabla 1. Estimaciones de d, *parámetro fraccionario diferencial, en algunas series ambientales frente al Perú.*

Series	Method Geweke and Porter-Hudak (1983)	Kashypa and Eom (1988)
Callao wind cubed	.554	.600
Callao transport	.592	.637
Trujillo wind cubed	.470	.509
Trujillo transport	.603	.652
Oceanic transport	.286	.310
Oceanic wind cubed	.210	.229
SOI	.340	.387

Biological Series

One of the obvious but major problems in studying fisheries is that it is rarely possible to obtain a reliable direct census of the fish population. Instead, "sampling" is used to obtain estimates. Usually the sampling scheme is of no statistical design, but instead depends on uncontrollable factors such as fishermen's behavior. The actual data, or the observables, are things like catch and effort statistics, length distributions, etc. While a variety of schemes have been devised to use this information to estimate characteristics of the population, the inescapable fact is that only the catch, effort, length distribution measurements, etc. are data, while the rest are estimates.

A property of calculating estimates from data is that degrees of freedom are used. In most cohort-analysis schemes, many degrees of freedom are used in calculating population and recruitment estimates. As the schemes are operating on autocorrelated data, they also act as filters on the observed data, changing the importance of different frequencies. When the same algorithm is used to jointly estimate many series, it is likely that just due to the estimation scheme, there will be a certain amount of cross-correlation in the resultant estimates.

It has been common to treat estimates of recruitments and of parents as data with the usual degrees of freedom. (Ultimately I will be forced to do the same (it is all there is to work with), but not without some careful checks on artificially-induced correlation.) In effect, when I use the recruitment estimates to estimate a relationship with another variable, I am fitting a composite function $f(g(x))$ of the original catch, effort and length data, where x is the original data, $g()$ is the operation performed by the cohort analysis, and $f()$ is the final relationship. If two intermediate estimates of this composite process exhibit a strong relationship, it cannot be said for certain that this relationship is real, or is just a product of the estimation scheme. Thus if parents and recruits are strongly related, it may be an artifice of cohort analysis. This will make it difficult to interpret many of the results to follow.

As mentioned previously, in attempting to correct for mortality other than from fishing, the resulting consumption estimates are functions of SST, and this feeds into the recruitment and parent estimates. Thus SST, and any variable highly correlated with SST, will have an unknown degree of spurious correlation with the population estimates. Most of the transport series display a reasonable degree of correlation with SST.

The new estimates of recruitment are shown on Fig. 7, along with the old ones. The new estimates exhibit less relative variation than do the original estimates, as was anticipated by Pauly (1987) who wrote that "it can be hypothesized that the [new] recruitment and biomass [....] will be somewhat smoother". Both series show an increase from 1957 to 1958, during El Niño, but in the original estimates this increase produced a change in mean level in both parent biomass and in recruitment, while in the new estimates the recruitment level drops right after the end of the El Niño. The new estimates start increasing from about 1963 to 1969-1970, after which both the new and old estimates show a similar decrease. The old estimates then show a more significant relative increase than do the new estimates. The parent biomass follows a similar pattern (Fig. 8).

The estimated AR component of the new recruitment estimates (Fig. 9) is relatively less variable than the AR component of the old estimates, particularly during the 1960s. The log of the ratio of recruits to parent biomass three months earlier (Fig. 10) is relatively constant except for the El Niño years of 1972 and 1982-1983. The ratio with the number of eggs shows a similar pattern (not shown), though the decrease during the 1972 El Niño is not as sharp. The spectrum of both the recruit series and the log of the recruits (Fig. 11), is dominated by a red noise component with a weak yearly signal.

The picture presented by these graphs is of a highly persistent, stable series where the only significant change occurred during a one or two year period around 1969. In fact, the trend in the new recruitment estimates mirrors closely what would be expected from the smoothed (5-year averaged) trends in catch and effort in Agüero (1987). After all the corrections, except for questions of scale, the recruitment estimates tend to mirror catch-per-unit-effort (C/f).

Some of the smoothness in the new recruitment estimates are due to mackerel consumption being a surrogate for SST (Pauly 1987). During El Niño years, for example, the catch rate tended to decrease. In the previous models, this results in variability in the recruitment estimate. In the

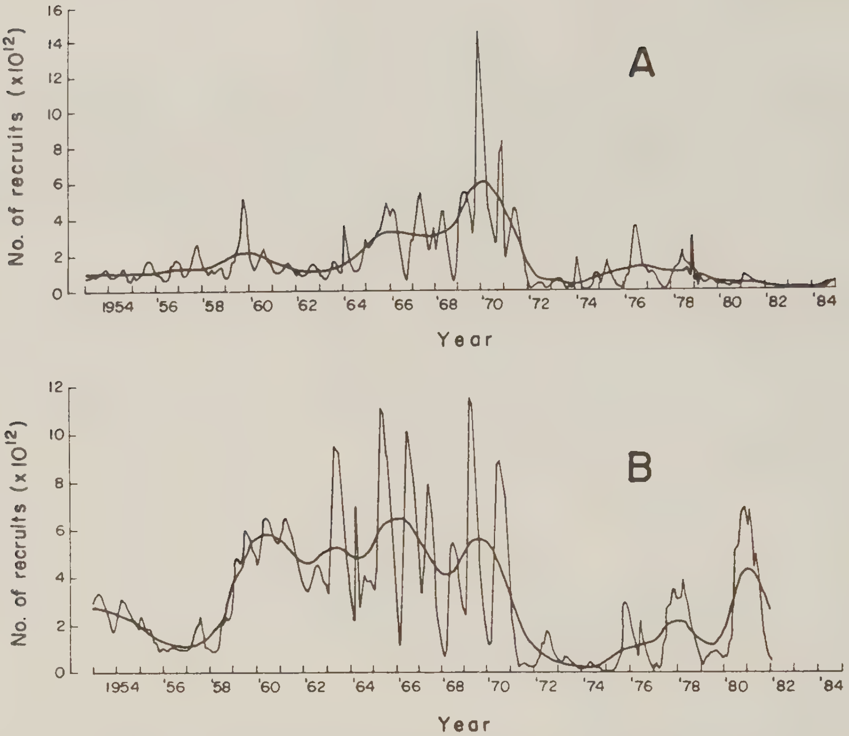


Fig. 7. Comparison of new (A) and old (B) recruitment estimates for the anchoveta, with estimated local trend lines.
Fig. 7. Comparación de las nuevas (A) estimaciones del reclutamiento de la anchoveta y los antiguos (B), con líneas de las tendencias locales estimadas.

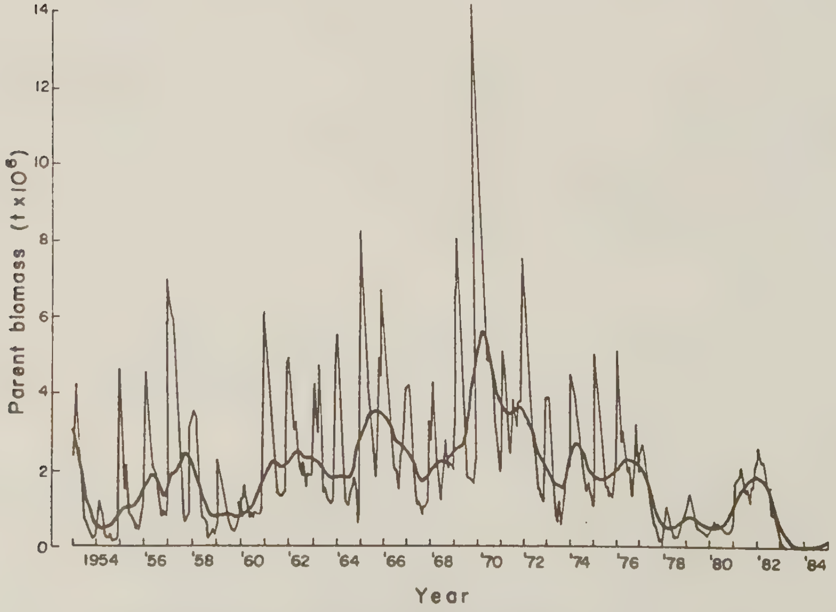


Fig. 8. New estimates of anchoveta parent biomass with estimated local trend.
Fig. 8. Nuevas estimaciones de la biomasa parental de anchoveta con estimación de la tendencia local.

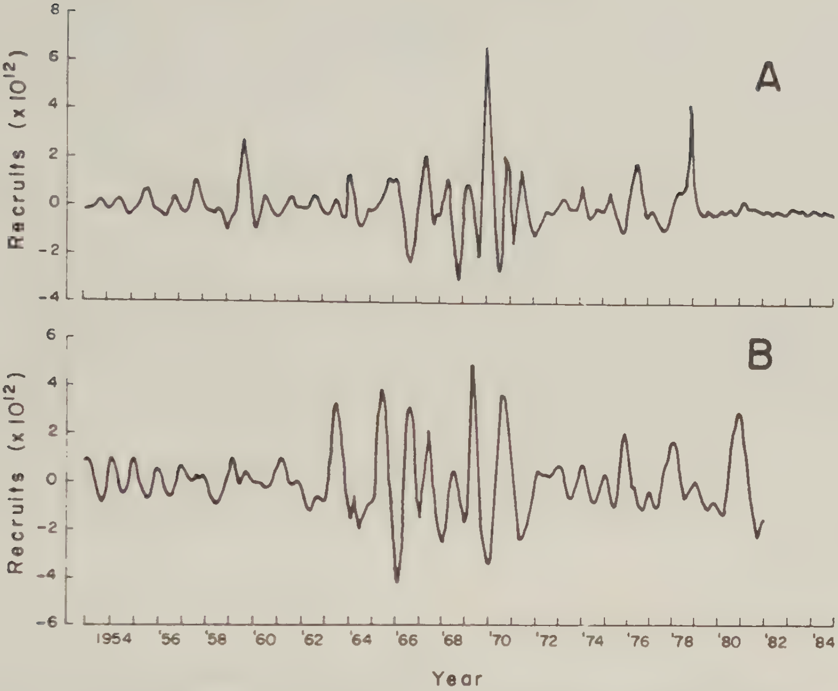


Fig. 9. Stationary (autoregressive) components of the new (A) and old (B) estimates of anchoveta recruitment.

Fig. 9. Componentes estacionarios (autoregresivo) de las nuevas (A) y antiguas (B) estimaciones del reclutamiento de anchoveta

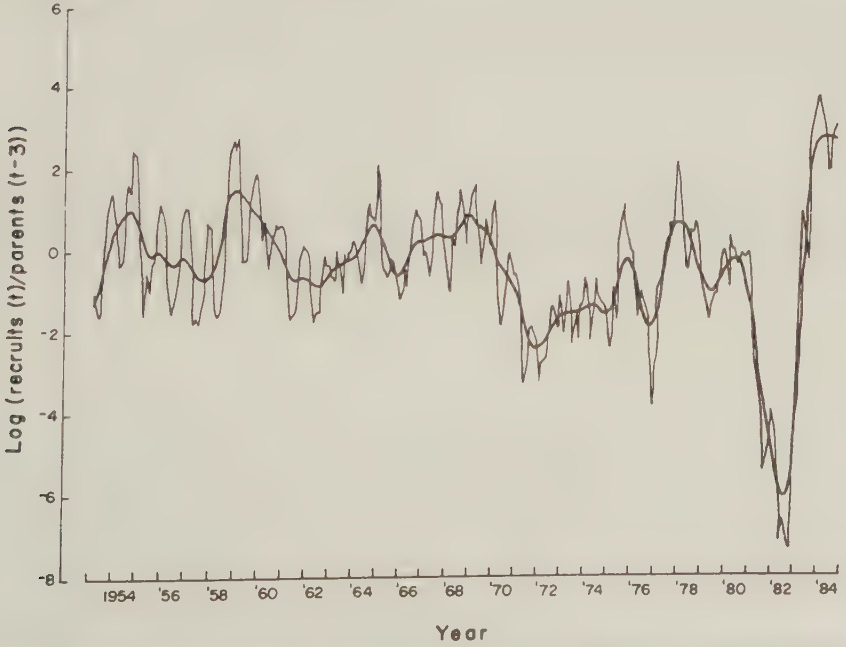


Fig. 10. The log of the ratio of the new recruitment estimates and parent biomass 3 months earlier, the estimated month of hatching.

Fig. 10. Logaritmo de la razón entre la nueva estimación de reclutamiento y biomasa de padres 3 meses antes (mes estimado de eclosión).

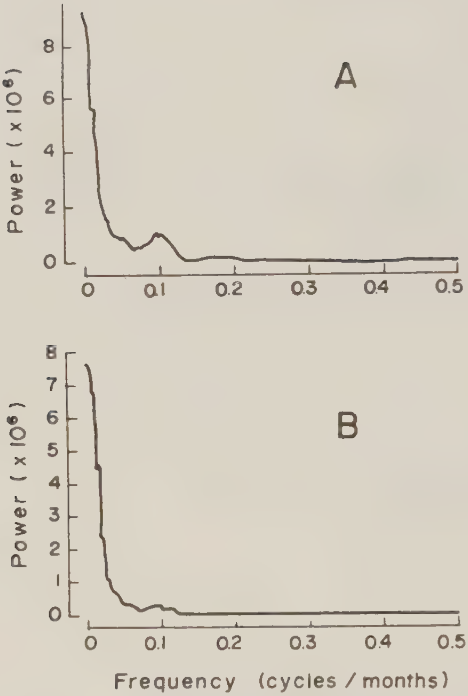


Fig. 11. Estimated power spectra for the new recruitment estimates (A) and for the log of the new recruitment estimates (B).

Fig. 11. Poder espectral estimado para las nuevas estimaciones de reclutamiento (A) y para el log de las nuevas estimaciones de reclutamiento (B).

new series, the mackerel are assumed to come closer to shore as SST warms, increasing mackerel consumption and thereby increasing the estimated population sizes. Mackerel consumption has prewhitened the inputs into the estimation algorithm based on the variation in SST. This does not necessarily mean that prewhitening the inputs is incorrect, but it does explain why there are such differences in the two sets of recruitment estimates.

Comparing the parent series (Fig. 8) with the ratio of recruits to parent biomass (Fig. 10), it is clear that the trend in the log of the ratio is largely explained by changes in the parent biomass, particularly if a mild density dependence is assumed. In the next section I will return to this point more formally, but it brings me back to the initial discussion of this section. If the estimated parent biomass and the estimated recruitment appear to be closely related, is it truly a feature of the population dynamics or a feature of the method that jointly estimates both series?

Data Analysis

In M&M it was found that the monthly recruitment estimates were so highly autocorrelated that it was necessary to examine the monthly series, mildly smoothed (two month nonoverlapping averages), across years. This allowed estimation of the interyear variability as well as to obtain some idea of the intrayear variability. The new recruitment estimates have an autocorrelation of .99 at a lag of 1 month. Even after first differencing, the series is still nonstationary, with the autocorrelations positive and significant at a lag of well over 20 months. This behavior in the autocorrelation function is expected, given the estimated spectrum of the series. Nonoverlapping averages can be formed to try to find a scale at which the series decorrelates and has a more stationary autocorrelation function. However, it is necessary to average almost on a yearly basis to achieve a reasonable degree of stationarity, at which point there is no reason to use anything except the yearly averages.

Following M&M, I have formed 2-month averages of recruitment and parent biomass, as December-January, February-March, etc. The value for December 1952-January 1953 is just the January value, as average, not total values, are used. Each of these series will be examined across years. Senocak et al. (this vol.), based on the egg survey data in Santander (1987), show that the bulk of the egg distribution throughout the year is inshore rather than offshore. From 1961-1972, for most months the center of the egg distribution is more northerly, around Trujillo rather than Callao. From 1972 onward, the center shifts, being at many times evenly distributed along the coast from Trujillo to Callao, or in some months, clearly centered at Callao. Given the differences in the dynamics of the wind data series analyzed above, this argues for using either the Trujillo or Callao series. As Trujillo is more of a center of the egg distribution in these charts than is Callao, transport at Trujillo, as in M&M, will be used as the environmental variable. As mentioned previously, when a nonlinear analysis is used, this cannot readily be resolved from turbulence at the same location.

Additive models were estimated for the log of recruitment as the response variable, with parent biomass 2 averaged time periods prior (June-July parent biomass predicts October-November recruitment etc.) and Trujillo transport in the previous September and November as the predictor variables. The results in M&M, in Cury and Roy (1989), and the graphical results above all suggest that recruitment should be modeled on a log scale. The span for the transformations of the parent biomass were chosen using cross-validation, which explicitly calculates a tradeoff between the degrees of freedom and the variance of the fit. The estimated transformations of parent biomass (Fig. 12) are approximately that of a log transformation in each case. Thus on a log-log scale, for the period April through November, over 90% of the variance of the recruitment is explained by the parent biomass at the time of birth (Table 2).

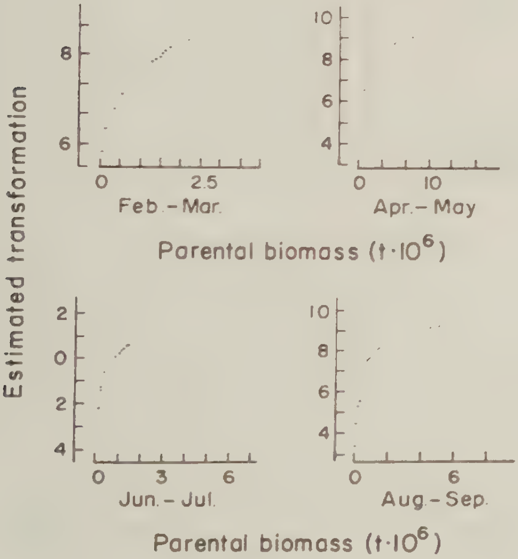


Fig. 12. Estimated transformations of the parent biomass when predicting anchoveta recruitment in a generalized additive model. All four transformations are close to a log transformation.

Fig. 12. Transformaciones estimadas de la biomasa parental cuando se pronostica el reclutamiento de anchoveta en un modelo aditivo generalizado. Las cuatro transformaciones son próximas a la transformacion logaritmica.

For the period from December through March, the estimated r^2 is around .60 (Table 3). The period from December through March is the period of lowest recruitment (Fig. 13A). Therefore the additive models work best during the most important periods of recruitment. On a log scale (Fig. 13B), the monthly recruitment values underline what I have said previously. Recruitment was fairly constant until 1969, with a big peak in 1969, followed by a drop to a new equilibrium

It is entirely possible that recruitment is tightly coupled to parent biomass as these models suggest. That then leaves open the question of why there was such a large parent biomass in 1969. Certainly the recruitment feeding into that year was nothing special compared to previous years; and graphs of the possible environmental factors by month (not shown), do not reveal anything unusual at this time period. The other possibility, of course, is that this is a feature of jointly estimating parents and recruits on such a fine time scale. The added degrees of freedom seemingly brought about from monthly recruitment estimates, at least for the purposes of this

Table 2. Analysis of Deviance for Recruitment-Parent Biomass Models, April-November.
Tabla 2. Análisis de desviaciones para el modelo de Reclutamiento-Biomasa parental, Abril-Noviembre.

```
response variable .... April-May Recruits
deviance  =  10.577 # iterations  =  1 #smooths/variable =,  1
average deviance  =  .353
dof of deviance   26.77 scale estimate                              .395
r square = 84.01% of a null deviance of                           66.169

        span          dof            slope                     name
        ----          -----          --------          ------------------------------------
         --            1             7.3602            s0---the intercept term
        .60           2.234          smooth            cv: Dec-Jan Parent Biomass

response variable .... June-July Recruits
deviance  =  2.966 # iterations  =  1
#smooths/variable =,  1
average deviance  =  .099
dof of deviance  24.83 scale estimate              .119
r square = 95.67% of a null deviance of          68.493

        span          dof            slope                     name
        ----          -----          --------          ------------------------------------
         --            1             7.4202            s0---the intercept term
        .30           4.166          smooth            cv: Feb-Mar Parent Biomass

response variable .... August-September Recruits
deviance  =  1.569 # iterations  =  1
#smooths/variable =,  1
average deviance  =  .052
dof of deviance  24.67 scale estimate              .064
r square = 97.73% of a null deviance of          69.229

        span          dof            slope                     name
        ----          -----          --------          ------------------------------------
         --            1             7.4654            s0---the intercept term
        .30           4.331          smooth            cv: Apr-May parent Biomass

response variable .... October-November Recruits
deviance  =  5.830 # iterations  =  1
#smooths/variable =,  1
average deviance  =  .194
dof of deviance  24.78 scale estimate              .235
r square = 92.62% of a null deviance of          79.032

        span          dof            slope                     name
        ----          -----          --------          ------------------------------------
         --            1             7.3894            s0---the intercept term
        .30           4.220          smooth            cv: Jun-Jul Parent Biomass
```

Table 3. Analysis of Deviance for Recruitment-Parent Biomass Models, December-March.
Tabla 3. Análisis de desviaciones para el modelo de Reclutamiento-Biomasa parental, Diciembre-Marzo.

```
response variable .... December-January Recruits
deviance  =  28.488 # iterations =  1
#smooths/variable =,  1
average deviance =  .950
dof of deviance  26.74 scale estimate              1.065
r square = 60.05% of a null deviance of           71.313

        span          dof            slope                     name
        ----          -----          --------          ------------------------------------
         --            1             7.2947            s0---the intercept term
        .70           2.257          smooth            cv: Aug-Sep Parent Biomass

response variable .... February-March Recruits
deviance =  26.553 # iterations =  1
#smooths/variable =,  1
average deviance =  .885
dof of deviance  26.90 scale estimate               .987
r square = 59.44% of a null deviance of           65.465

        span          dof            slope                     name
        ----          -----          --------          ------------------------------------------
         --            1             7.3055            s0---the intercept term
        .60           2.097          smooth            cv: October-November Parent Biomass
```

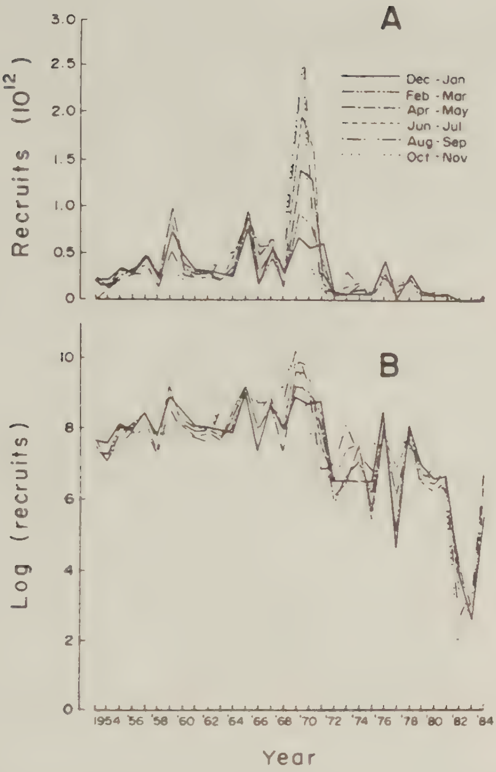


Fig. 13. Time series of bimonthly anchoveta recruitment and the log of bimonthly anchoveta recruitment.

Fig. 13. Serie de tiempo de reclutamiento bimensual de la anchoveta y el logaritmo del reclutamiento bimensual.

paper, do not seem to be there. It appears that all the adjustments in the estimates, while perhaps revealing interesting features in the dynamics of anchoveta recruitment, have also limited the amount of independence in the data.

Cury and Roy (1989) estimate transformations for the yearly averages for the old estimates using the ACE algorithm of Breiman and Friedman (1985). For completeness, I have redone this for the new recruitment estimates (Fig. 14A). Cury and Roy's basic conclusions remain unchanged. The ACE algorithm does not provide an analysis of variance, and given the correlation between transport and turbulence at Trujillo, starting with the variable of lower dimension appears wise. For this reason I refit this model using generalized additive models.

The analysis of deviance for a span of .20 (Table 4) shows that the single best predictor is transport, which for this choice of span explains 60% of the variance. With so few data points, the fit does vary with the choice of span, from roughly 50% to 60%. In all cases, however, the fit due to transport was much higher than that due to parent biomass. When both variables are included, the r^2 increases to .78, which suggests that there is also strong intercorrelation between the parent biomass estimate and turbulence. The range of r^2 for different values of the span was .68 to .78.

The estimated transformations (Figs. 14B and 14C) for both variables resemble a log transformation, and the 95% confidence intervals (Hastie and Tibshirani 1985) are reasonably tight around the mean and preserve the same shape. While the choice of span affects the estimated degrees of freedom, the shape of the transformation is unaffected by the choice of span.

The effect of the transformations can also be viewed by fitting a smoothed surface to the 3-dimensional data (Fig. 15). (This is also a phase plot of recruitment for both datasets). The transformed surface is unimodal and smoother. It is clear that the relationships on the raw scale are nonlinear, while those on the transformed scale are linear in each dimension. While the model is only an additive approximation, it has caught the essence of what information is contained in the data.

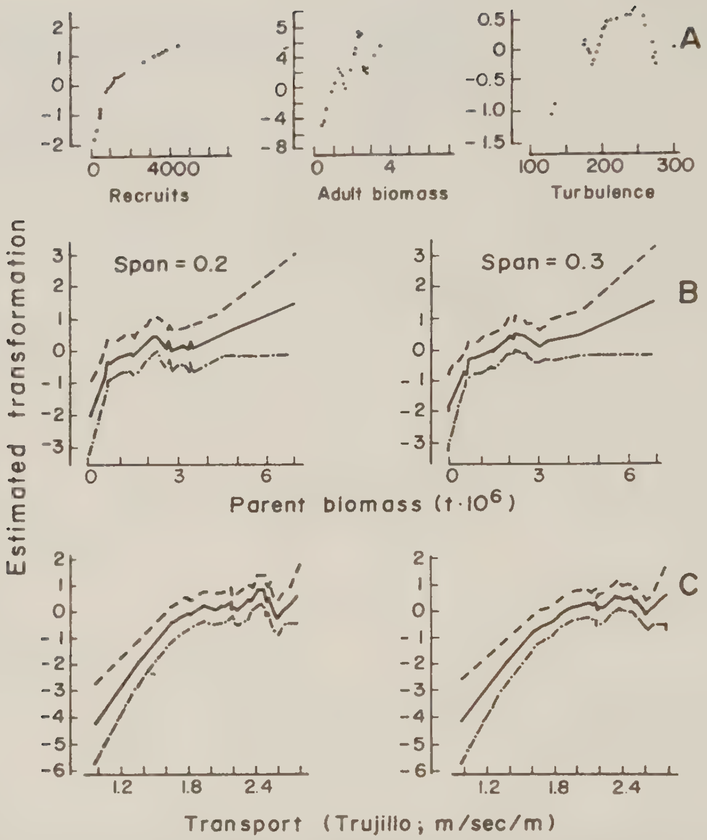


Fig. 14. Estimated transformations (A) from the ACE algorithm, redoing the analysis of Cury and Roy (1989) for the new recruitment estimates. (B) Parent biomass in a generalized additive model for predicting yearly anchoveta recruitment. Dashed lines are 95% confidence intervals for the transformations. (C) Trujillo transport in a generalized additive model for predicting yearly anchoveta recruitment. Dashed lines are 95% confidence intervals for the transformations.

Fig. 14. Transformaciones estimadas (A) del algoritmo ACE, rehaciendo el análisis de Cury y Roy (1989) para las nuevas estimaciones del reclutamiento. (B) Biomasa parental en un modelo aditivo generalizado para predecir el reclutamiento anual de la anchoveta. Las líneas punteadas representan el intervalo de confianza del 95% para las transformaciones. (C) Transporte de Trujillo en un modelo aditivo generalizado para predecir el reclutamiento anual de la anchoveta. Las líneas punteadas representan el intervalo de confianza del 95% para las transformaciones.

Discussion

I have shown that the new estimates of recruitment are much smoother than the previous estimates, with different trends, except for the sharp decrease following 1969 evident in both sets of estimates. Part of the difference between the two sets of recruitment estimates appears to be due to the fact that several estimates of anchoveta consumption, particularly that for mackerel, are surrogates for SST and tend to cause the recruitment estimates to be filtered (smoothed) based on the variation in the SST series.

The new recruitment estimates, even more so than the previous estimates, are highly autocorrelated, even after differencing. Essentially all of the variance in the monthly recruitment series can be modeled by a simple AR(1) model. It is questionable that this represents the true dynamics of recruitment, and certainly would follow, rather than predict, any sudden changes in the population dynamics. Nonoverlapping time averaging requires forming yearly averages to achieve a satisfactory level of stationarity.

Table 4. Analysis of Deviance for Recruit-Parents-Transport Model, Yearly Data.
Tabla 4. Análisis de desviaciones para el modelo de Reclutamiento-Padres-Transporte, datos anuales.

```
response variable .... LOG (RECRUITS)
deviance = 32.239 # iterations = 1
#smooths/variable =, 1
average deviance = 1.007
dof of deviance 25.27 scale estimate          1.276
r square = 45.37% of a null deviance of      59.017

        span        dof           slope                      name
        ----        -----         -------          -----------------------------
        --          1             6.8277           s0---the intercept term
        .20         5.729         smooth           PARENT BIOMASS

response variable .... LOG (RECRUITS)
deviance = 22.121 # iterations = 1
#smooths/variable =, 1
average deviance = .691
dof of deviance 25.57 scale estimate           .865
r square = 62.52% of a null deviance of      59.017

        span        dof           slope                      name
        ----        ----          -------          -----------------------------
        --          1             6.8277           s0---the intercept term
        .20         5.435         smooth           TRANSPORT

response variable .... LOG (RECRUITS)
deviance = 12.714 # iterations= 1
#smooths/variable =, 6
average deviance = .397
dof of deviance 19.84 scale estimate           .641
r square = 78.46% of a null deviance of      59.017

        span        dof           slope                      name
        ----        -----         --------         -----------------------------
        --          1             6.8277           s0---the intercept term
        .20         5.729         smooth           PARENT BIOMASS
        .20 ·       5.435         smooth           TRANSPORT
```

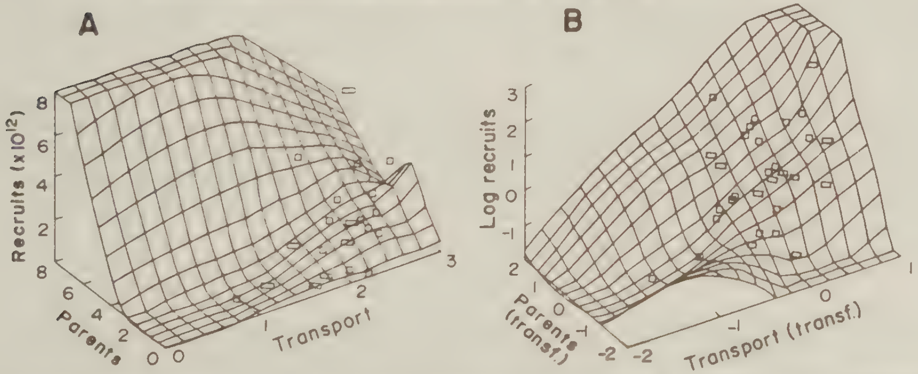


Fig. 15. Estimated smoothed surfaces for (A) yearly anchoveta recruitment, yearly parent biomass and Trujillo transport and (B) the estimated transformed data for the same variables. The small rectangles are the observed points. The effective linearization brought about by the transformations is immediate.

Fig. 15. Superficies suavizadas estimadas para (A) reclutamiento anual de la anchoveta, biomasa parental anual y transporte en Trujillo y (B) estimado de los datos transformados para las mismas variables. Los rectángulos pequeños son los puntos observados. La linealización efectiva producida por las transformaciones es inmediata.

Bimonthly averages of recruitment, viewed across years, are extremely correlated with the log of parent biomass when the recruits were born. The high degree of fit is suspicious, and may be due to the fact that both series were jointly estimated. This left little choice but to analyze yearly averages.

A generalized additive model was then estimated for the yearly averages, using the average parent biomass over the year, and the average transport at Trujillo. The resulting estimates suggest that on a nonlinear scale, about 75% of the variance in the recruitment estimates can be explained by these two series. The analysis suggests that large parent biomass, and a reasonable level of transport produce the best recruitment. Evidence is presented that these nonlinear estimates are relatively stable.

Parrish et al. (1984) argue that transport should be an important variable in the Peruvian system, but due to the dominance of wind in a single direction, it is not possible to resolve whether it is transport, turbulence or some combination of the two (as argued by Cury and Roy 1989) affecting the fish. Even at the yearly scale it is not possible to say what part of the relationship between the parent biomass and the recruitment estimates are due to correlation from their joint estimation. This is compounded by the fact that transport is correlated with SST, and all the population estimates have been influenced by changes in SST.

Unlike in M&M, the present model, if valid, has much explanatory power but little predictive use since all terms are contemporaneous and are averaged over a year. It may well be possible to construct models that will forecast using lagged terms to approximate the proper model, but it would be premature to do so at this time. More important at the moment is to study the various methods of cohort analysis to obtain either theoretical or empirical estimates of the expected cross-correlation functions between recruits and parents due to the fact that they are being jointly estimated in a model that uses up most of the degrees of freedom in the data. (Simulations based on model-generated data with recruitment a random variable, possibly autocorrelated, could give estimates of the expected level of correlation when none is present.) Further, some estimates of the likely base level of correlation with any environmental variable correlated with SST should also be ascertained.

With these results, more valid estimates of significance of a model would be possible. The yearly model in this paper, on the surface, has an intuitive biological interpretation, but this does not guarantee its validity. If all the new population estimates are valid, the existing interpretations of what has occurred in the anchoveta fishery would have to be greatly modified. The new estimates suggest a population that essentially stays in equilibrium until some single event changes the mean level. A new mean level is then found, until another shock comes to the system. The most likely cause of these shocks are environmental changes, but as examined here and in Bohle-Carbonell (this vol.), the environment around Peru exhibits long-term memory, so that monitoring of the environment would have to become an important part of the predictive process.

This implies that once local mechanistic models can be validated, then the use of surrogate variables, such as SOI, that may "monitor" the ocean further ahead, could be useful in forming a predictive model. I have not examined this possibility in detail, but I have presented evidence based on the interrelationship between the SOI and oceanic transport, that this longer lead prediction is at least physically plausible.

Acknowledgements

I thank Dr. Daniel Pauly for inviting this contribution, and Mr. Jaime Mendo for discussions and insights into the Peruvian anchoveta fishery. My colleagues at PFEG have provided helpful comments on earlier drafts. The GAIM program used to estimate the generalized additive models was provided by Drs. Trevor Hastie and Robert Tibshirani. Rob Tibshirani has generously answered questions about the program.

References

Akaike, H. 1977. On entropy maximisation principle, p. 27-41. *In* P.R. Krishnaiah (ed.) Applications of Statistics. North-Holland, Amsterdam.

Agüero, M. 1987. A bioeconomic model of the Peruvian pelagic fishery, p. 307-324. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Bakun, A. 1987. Monthly variability in the ocean habitat off Peru as deduced from maritime observations, 1953-84, p. 46-74. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Bakun, A. and R.H. Parrish. 1982. Turbulence, transport, and pelagic fish in the California and Peru Current systems. CalCOFI Rep. 23: 99-112.

Bloomfield, P. 1976. Fourier analysis of time series: an introduction. John Wiley and Sons, New York. 258 p.

Brainard, R.E. and D.R. McLain. 1987. Seasonal and interannual subsurface temperature variability off Peru, 1952 to 1984, p. 14-45. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Breiman, L. and J.H. Friedman. 1985. Estimating optimal transformations for multiple regression and correlation (with discussion). J. Am. Stat. Assoc. 80: 580-619.

Cleveland, W.S. 1979. Robust locally weighted regression and smoothing scatterplots. J. Am. Stat. Assoc. 74: 829-836.

Cury, P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Can. J. Fish. and Aquat. Sci. 44: 670-680.

Geweke, J. and S. Porter-Hudak. 1983. The estimation and application of long memory time series models. J. Time Series Anal. 4: 221-238.

Granger, C.W.G. and R. Joyeux. 1980. An introduction to long memory time series models and fractional differencing. J. Time Series Anal. 1: 15-29.

Hastie, T. 1987. A closer look at deviance. The Am. Stat. 41: 16-20.

Hastie, T. and R. Tibshirani. 1985 Generalized additive models: some applications, p. 66-81. *In* R. Gilchrist, B. Francis, and J. Whittaker (eds.) Generalized Linear Models. Springer-Verlag Lecture Notes in Statistics 32. Springer, New York.

Hastie, T. and R. Tibshirani. 1986. Generalized additive models (with discussion). Statistical Science 1: 297-318

Hosking, J.R.M. 1981. Fractional differencing. Biometrika 68: 165-176.

Hurst, H.E. 1951. Long term storage capacity of reservoirs. Trans Am. Soc. Civil. Engrs. 116: 770-799.

Kashypa, R.L. and Kie-Bum Eom. 1988. Estimation in long-memory time series models. J. Time Series Anal. 9: 35-42.

Kitagawa, G. and W. Gersch. 1984. A smoothness priors - state space modeling of time series with trend and seasonality. J. Am. Stat. Assoc. 79: 378-389.

Kohn, R. and C.F. Ansley 1988. The equivalence between Bayesian smoothness priors and optimal smoothing for function estimation, p. 393-430. *In* J. Spell (ed.) Bayesian Analysis of Time Series and Dynamic Models, Marcel Dekker, New York.

Lasker, R. 1978. The relation between oceanographic conditions and larval anchovy food in the California current: identification of factors contributing to recruitment failure. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 173:212-230.

Mandelbrot, B.B. 1971. A fast fractional Gaussian noise generator. Water Resour. Res. 7: 543-553.

Mandelbrot, B.B. 1983. The Fractal Geometry of Nature. W.H. Freeman and Company, New York. 468 p.

Mandelbrot, B.B. and J.W. Van Ness. 1968. Fractional Brownian motion, fractional noises and applications. SIAM Review 10: 422-437.

Mendo, J., L. Pizarro and S Castillo 1987. Monthly turbulence and Ekman transport indexes, 1953 to 1985, based on local wind records from Trujillo and Callao, Peru. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling Ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Peru; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Mendelssohn, R. and J. Mendo. 1987 Exploratory analysis of anchoveta recruitment off Peru and related environmental series, p. 294-306. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft fur Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P. and H. Fuentes. 1987. Sea Lion and fur seal predation on the Peruvian anchoveta, 1953 to 1982, p. 234-247 *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú, Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P. and D. Pauly. 1987. Monthly anchoveta consumption of guano birds, 1953 to 1982, p. 219-233. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Muck, P. and G. Sánchez. 1987. The importance of mackerel and horse mackerel predation for the Peruvian anchoveta stock (a population and feeding model), p. 276-293. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D. 1987. Managing the Peruvian upwelling ecosystem: a synthesis, p. 325-342. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly D. and I. Tsukayama, Editors. 1987. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Pauly, D., A. Ch. Vildoso, J. Mejía, M. Samamé and M.L. Palomares. 1987. Population dynamics and estimated anchoveta consumption of bonito *(Sarda chiliensis)* off Peru, 1953-1982, p. 248-267. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Parrish, R.H., A. Bakun, D.M. Husby and C.S. Nelson. 1984. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction, p. 731-777. *In* G.D. Sharp and J. Csirke (eds.) Proceedings of the Expert Consultation to Examine Changes in Abundance and Species of Neritic Fish Resources. San José, Costa Rica, 18-29 April 1983. FAO Fish. Rep. 291 (Vol. 3).

Porter-Hudak, S.L. 1982. Long-term memory modeling - a simplified approach. Ph.D. thesis, Dept. of Statistics, University of Wisconsin, Madison.

Santander, H. 1987. Relationship between anchoveta egg standing stock and parent biomass off Peru, 4-14 S. p. 179-207. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Schwarz, G. 1978. Estimating the dimension of a model. Ann. Statist. 6: 461-464.

Temporal and Spatial Dynamics of a Coastal Pelagic Species, *Sardinella maderensis* off the Ivory Coast

Roy Mendelssohn

Pacific Fisheries Environmental Group, Southwest Fisheries Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, P.O. Box 831 Monterey, CA 93942 USA

and Philippe Cury

ORSTOM, Centre de Recherches Oceanographiques de Dakar-Thiaroye, B.P. 2241 Dakar, Senegal

Mendelssohn, R., and P. Cury. 1989. Temporal and spatial dynamics of a coastal pelagic species, *Sardinella maderensis* off the Ivory Coast. Can. J. Fish. Aquat. Sci. 46: 1686–1697.

Variations of fortnightly catch-per-unit-effort (CPUE) of *Sardinella maderensis* off the Ivory Coast is studied both in time and in space–time. Using multivariate time series models, lagged values of coastal sea surface temperature (SST) and salinity explain 33% of the variation of CPUE during this period. When optimal transformations are estimated, 55% of the variance is explained. The optimal transformations suggest that good catch rates are associated with local upwelling or oceanic frontal structures. However, the model differs significantly from previous models that examine the CPUE for the combined catches of the fleet. The model is shown to produce reasonable forecasts for the next two years. In space–time, evidence is presented that suggests that the migration of the fish between areas is related to movement of structures in the ocean. The relationships between CPUE and the environment are again highly nonlinear, so that linear analysis, such as correlation analysis, will be of limited use in examining these questions.

On étudie dans le temps ainsi que dans l'espace et le temps les variations des prises par unité d'effort (PPUE) de *Sardinella maderensis* observées à tous les quinze jours au large de la Côte d'Ivoire. Quand on utilise des modèles de séries chronologiques à plusieurs variables, les valeurs décalées de la TMS et de la salinité près des côtes expliquent 33 % de la variation des PPUE observée pendant cette période. L'estimation des transformations optimales permet d'expliquer 55 % de la variance. Ces transformations donnent à penser que de bons taux de capture sont associés à une remontée locale ou à des fronts océaniques. Cependant, le modèle diffère sensiblement des modèles précédents qui étudient les PPUE en fonction des prises regroupées de la flottille. On montre que le modèle fournit des prévisions raisonnables pour les deux prochaines années. Sur le plan spatio-temporel, on présente des faits qui portent à croire que la migration de ce poisson entre les secteurs est liée au déplacement de structures dans l'océan. Les relations fonctionnelles entre les PPUE et l'environnement sont une fois de plus fortement non linéaires, de sorte que l'analyse linéaire, comme l'analyse de corrélation, sera d'une utilité restreinte pour l'étude de ces questions.

Received June 9, 1987
Accepted May 29, 1989
(J9312)

Reçu le 9 juin 1987
Accepté le 29 mai 1989

In a previous paper (Mendelssohn and Cury 1987) we studied the temporal dynamics of the combined pelagic species of the fishes off the Ivory Coast and how environmental processes affected the combined species dynamics, ignoring any spatial dynamics. There is reason to believe, however, that the dynamics of the combined species, which is of the greatest importance to the fleet, may differ from the dynamics of any individual species. If the biology of the individual species differs significantly, only broad oceanographic processes may appear to be affecting the dynamics, while different, more local processes may be affecting a particular species. Therefore, in this paper, we focus our attention on the dynamics of the catch rates of the dominant pelagic species caught in this area, *Sardinella maderensis*.

Determining the factors that affect changes in pelagic fish abundance, availability, and distribution, is complicated since the fish show a preference both for certain contemporaneous environmental conditions as well as for a particular history of the water masses and their food content (Mendelssohn and Roy 1986; Cury and Roy 1987; Mendelssohn and Cury 1987). A purely spatial analysis would blur these features, suggesting little relationship with the environment. Thus a dynamic, temporal approach is required.

The continental shelf off the Ivory Coast is affected by two upwelling seasons: a main season that occurs around June to September and a weaker, shorter season around January and February (Morlière 1970; Picaut 1983). Both sea surface temperature and salinity in this area vary seasonally and the intra-year variability in fish availability has been shown to be influenced by this variability (Marchal 1967). Marchal and Picaut (1977) present evidence that the strength of the local upwelling off the Ivory Coast, which is partly influenced by the configuration of the continental shelf, induces differential pelagic fish distributions. These fish distributions will fluctuate in space due to the dynamics of the water masses (Marchal 1967; ORSTOM/FRU 1976). Thus a temporal approach by itself also is not sufficient to explain the variability in fish availability — a spatial approach is required.

Understanding intra-year variations in indices such as catch-per-unit effort (CPUE) that reflect availability or abundance of a fish species is important to fisheries management. Studies have suggested that environmental conditions affect availability and hence fishing success (see for example Belvèze and Erzini 1983). During any given year there are probably several environmental factors that may influence fish availability, such as: sea temperature, salinity, dissolved oxygen, water mass boundaries, color and turbidity of the water, river outflows etc. (Bakun and Parrish 1980; Laevastu and Hayes 1981). Robust forecasts for fisheries need to be based on an understanding of the processes involved and should also help to clarify and increase our understanding of how the climatic factors influence the fish population.

Our interest in this paper is to determine the environmental processes that are important to the dynamics of *S. maderensis*, the form of these relationships, and to see to what extent spatial aggregation of fisheries data distorts these relationships. We analyze, using catch rate data, the changes in CPUE of this species through time, treating the entire area in aggregate, as well as the spatial–temporal dynamics of the species, that is the changes in time as well as the simultaneous changes in the distribution in space. As indicators of the environment we use sea surface temperature (SST), the sea temperature at 5 m depth (SST5M) and salinity at 5 m depth (SAL5M). These variables are chosen because they are the most complete and readily available environmental series and because they tend to reflect broad changes in the ocean environment.

Our models lead us to the conclusion that the dynamics of an individual species may differ considerably from that of an assemblage of related species. The interpretation of possible causal mechanisms affecting the population dynamics also differs when we examine the species in space and time, rather than in either dimension alone. We also examine the ability of the spatially aggregated model to provide forecasts of future catch rates.

Methods

As in our previous paper, our main methods of analysis are multivariate time series techniques. We fill in missing data using an algorithm of Shumway and Stoffer (1982). This algorithm fits to the data an autoregressive (AR) model (in this case of lag 2) of the form:

$$(1)\quad x(t)=Ax(t-1)+w(t)$$

$$(2)\quad y(t)=Hx(t)+v(t),$$

where $x(t)$ is a p-dimensional vector of the underlying population at time t, $y(t)$ is a q-dimensional vector of the observed data, H is a $q\times p$ known matrix, A is a $p\times p$ matrix of parameters to be estimated, $w(t)$ is an independent, identically distributed random vector distributed as normal $(0,Q)$ and v is an independent, identically distributed random vector distributed as normal $(0,R)$. The algorithm uses a variant of the EM algorithm (Dempster et al. 1977) to find maximum likelihood estimates of A, Q, and R as well as minimum mean square estimates of the $x(t)$. A rationale for using AR(2) models is given in Mendelssohn and Cury (1987).

To find local trend lines in the data we use the LOWESS scatterplot smoother (Cleveland 1979). This smoother is a two pass algorithm. In the first pass, each point is estimated using a weighted regression of all points within a given neighborhood of the point to be estimated. The second step corrects the estimate for outliers.

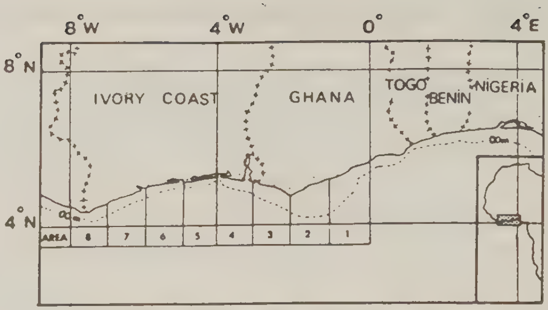


FIG. 1. Location of areas studied off the Ivory Coast.

Given data from a set of k time series, we consider a class of stochastic difference equations called vector autoregressive moving average models (or ARMA models for short) of the form (Tiao and Box 1981)

$$(3)\quad \Phi_p(B)z_t=\Theta_q(B)a_t,$$

where

$$(4)\quad \Phi_p(B)=I-\Phi_1B-\ldots-\Phi_pB^p,$$

$$(5)\quad \Theta_q(B)=I-\Theta_1B-\ldots-\Theta_qB^q$$

are matrix polynomials in B, the Φ's and Θ's are $k\times k$ matrices, $z_t=Z_t-\eta$ is the vector of deviations from some origin η that is the mean if the series is stationary, and $\{a_t\}$ with $a_t=(a_{1t},\ldots,a_{kt})$ is a sequence of random shock vectors, identically, independently and normally distributed with zero mean and covariance matrix Σ. We follow the identification and estimation scheme described in Tiao and Box (1981) and Tiao et al. (1980), also used in our previous paper (Mendelssohn and Cury 1987).

We emphasize that throughout the paper we fit true multivariate models, not transfer-function or so called ARMAX models. There are some technical differences between the two models, which are most important when we are looking at space–time dynamics and are modeling both CPUE and the environment. Vector ARMA models, since they include the interaction between all the variables, tend to better take into account the intercorrelations between various different environmental series. These points are discussed further in Tiao and Box (1981, p. 804) and in Tiao et al. (1980).

At points in the paper we also use a subset autoregression procedure developed by Akaike (Akaike et al. 1979) to help identify the appropriate model form for estimation. This is a complicated procedure based on the Householder transformation and the AIC information measure and the reader is referred to the reference for a complete description of it.

Most techniques such as regression fit a linear, additive model to the data of the form

$$(6)\quad y(t)=u+\sum_{i=1}^{N}\beta_i x_i(t)+e(t).$$

A simple, natural extension is to fit additive models of the form

$$(7)\quad T(y(t))=a+\sum_{i=1}^{N}s_i(x_i(t))+h(t),$$

where $T(\ )$ and the $s_i(\ )$ are possible nonlinear transformations

TABLE 1. Values of the coefficients of the multivariate AR(2) model used to estimate missing values in the CPUE time series.

	Area 4 CPUE		Area 5 CPUE		Area 6 CPUE		Area 7 CPUE	
Area	$(t-1)$	$(t-2)$	$(t-1)$	$(t-2)$	$(t-1)$	$(t-2)$	$(t-1)$	$(t-2)$
4	0.03	0.04	−0.05	0.04	−0.19	0.43	0.29	0.29
5	−0.05	0.02	0.03	0.02	0.02	0.27	0.05	0.13
6	0.04	0.02	0.02	0.13	0.36	0.22	0.04	−0.01
7	0.08	0.08	0.10	−0.19	−0.22	0.51	0.26	0.42

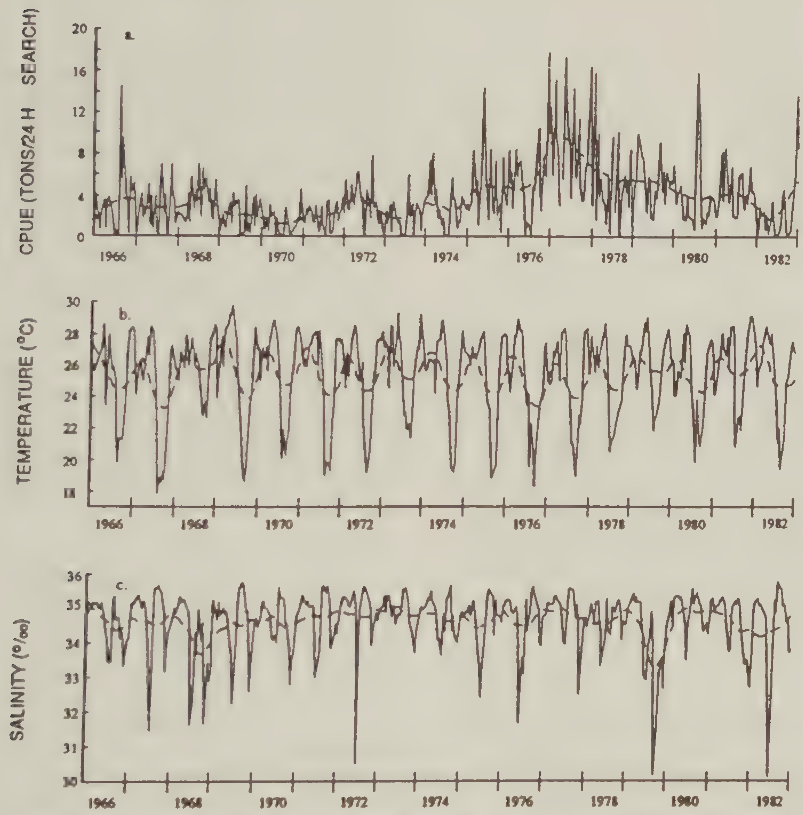


FIG. 2. Time series and estimated local trend for (a) aggregate CPUE, (b) SST, and (c) salinity.

of the data. In most problems, the form of these functions is not known a priori. The ACE (Alternating Conditional Expectations) algorithm of Breiman and Friedman (1985) empirically estimates the transformations that will have the smallest normalized residual error. In the bivariate case, this is equivalent to finding the transformations that produce the highest correlation. As the method is empirical, the form of each transformation is found by plotting the transformed data versus the original data. In the fisheries literature this algorithm has been used successfully by Mendelssohn and Cury (1987) and Mendelssohn and Mendo (1987).

Data

Biological Data

The pelagic fishery off the Ivory Coast has been described previously (Marchal 1967; FAO 1974, 1982), and Fonteneau and Marchal (1970) describe the data collection and data summarization procedures. *Sardinella maderensis* is the primary species exploited by the purse seiners based in Abidjan. The average annual landings of *S. maderensis* are about 10 000 t (mean for 1966–82); this is approximately 50% of the total Ivoirian catch of small pelagic species.

For purposes of our analysis, the Gulf of Guinea off the Ivory Coast was divided into eight areas each one degree in longitude and extending from 4°N of latitude to the coastline (Fig. 1). Measures of effort based on the time the boats spent searching for fish have been calculated using the method described in Fonteneau and Marchal (1970). CPUE for areas 4 to 7 was calculated for each fortnight from 1966 to 1982. (Fortnights in this context are periods of one-half month, not of 2 wk. Therefore each "fortnight" can vary in duration by up to several

TABLE 2. Parameters estimate and SE of the model using SST5M and SAL5M time series.

	Period 1966–1982		
Lag	Parameters	Estimate	SE
1	LNCPUE	0.304	0.049
	SST5M	−0.057	0.025
	SAL5M	0.028	0.012
2	LNCPUE	0.144	0.048
	SST5M		
	SAL5M		
4	LNCPUE		
	SST5M		
	SAL5M	−0.098	0.042
5	LNCPUE		
	SST5M	−0.078	0.026
	SAL5M	0.120	0.053
6	LNCPUE	0.192	0.046
	SST5M		
	SAL5M	0.073	
13	LNCPUE		
	SST5M	−0.062	0.014
	SAL5M		

days). Areas 4 to 7 are those where most of the catch of *S. maderensis* was taken. CPUE for each area was calculated by dividing the total catch in that area by the total search time for the boats in that area for the entire fortnight.

Mendelssohn and Cury (1987) discuss this measure of CPUE and possible problems that can arise when using it as a measure of local abundance. These problems are further compounded in this instance because it is not clear how to partition the measure of effort to reflect the effort expended only for *S. maderensis*. Using total effort as we do in this paper is not a completely satisfying alternative, because the fishermen fish for many species and for many periods, so the level of effort may be independent of the abundance of *S. maderensis* due to the presence of other species in the area.

The CPUE time series has missing data points, because an absence of fishing effort does not necessarily imply an absence of fish. Each of the areas 4–7 has about 10% of the data missing. The estimated parameters of the AR(2) model given in equations (1) and (2), used to fill in the data (Table 1), suggest a west to east migration and possible return. For example, CPUE in area 4 is significantly influenced by CPUE in areas 6 and 7 both 1 and 2 fortnight earlier (the last four values of the first row of the table) while area 7 is influenced by the past history of areas 6 and 7 and to some extent that of area 5 (the last row of the table).

Use of the completed data series in forming the space–time model will introduce more bias than in Mendelssohn and Cury (1987), due to some circularity in the process. The missing values of CPUE are estimated by an AR(2) model based on CPUE in all the areas during the surrounding time periods. Thus estimates of inter-area migrations might be affected by the filled-in data. Also, as only one species is being investigated, there are many more periods where there was effort but no catch of this particular species. This increases the likelihood that the form of the relationships is nonlinear, and that simple linear tools such as correlation studies or regression-like models will not be adequate. However, as only 10% of the data are missing, the filled-in data would have to have high leverage to greatly affect the final parameter estimates. As a further assurance that the filled-in values have not unduly influenced our results, we checked the stability of our parameter estimates to the inclusion or deletion of data and compared our results for consistency with independent observations on the fishery.

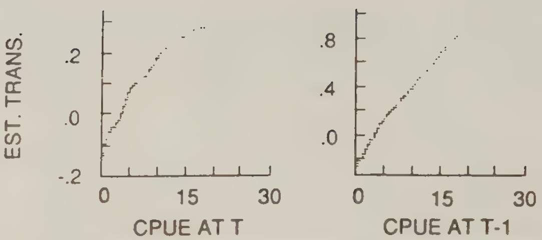


FIG. 3. Estimated optimal transformations of CPUE for predicting spatially aggregated CPUE.

The AR(2) model estimated by the missing data algorithm produces smoothed estimates of the data, including observation error. The smoothed values in each area (not shown) are close to the observed values when both exist and are consistent with other areas when one area has data and the second area does not. The completed time series of CPUE for each area were formed by substituting the smoothed estimate for each missing data point (see below).

A time series of CPUE aggregated across areas was calculated as the catch for all areas divided by the total effort (Fig. 2a). The localized trend, calculated using the LOWESS scatterplot smoother (Cleveland 1979), shows a slight dip in 1970, a slight rise and then a dip in 1972–73, and then a steady rise in CPUE to 1977. From mid-1977 onward, the trend has been downward until the start of an upturn in 1982.

Environmental Data

The environmental series consisted of SST data collected by merchant ships in the areas and SST5M and SAL5M collected by the Centre de Recherche Océanographique of Abidjan at a coastal station near Abidjan. Mean values were calculated for each fortnight to coincide with the fisheries data and missing data were filled in as in Mendelssohn and Cury (1987). SST aggregated across areas was calculated as the mean of the SST data by area.

The SST5M time series (Fig. 2b) shows a slight cooling trend until the end of 1967 followed by a slight warming trend until mid 1969. Since then there is no long-term trend in the data. The years 1969, 1973, 1978, and 1979 had noticeably warmer temperature minimums, while 1967 had a colder temperature minimum.

The SAL5M time series (Fig. 2c) also shows little long-term trend, except for sharp drops in 1968 and 1979. The years 1972, 1979, and 1982 also had significantly lower salinity minima.

Temporal Models of Aggregate Data

In this section we examine spatially aggregated CPUE for *S. maderensis* (actually we use $LNCPUE = \ln(CPUE + 0.5)$) and the environment. The approach of this section closely parallels Mendelssohn and Cury (1987) so that we can illuminate the differences between the dynamics of the dominant, more coastal *S. maderensis* from the dynamics of the combined species, many of which are more oceanic.

Identification

Sardinella maderensis is a more coastal species than some of the other pelagic species, and SST averaged over such a wide area is not a very accurate reflection of the conditions faced by a stock which only is fished near the coast. Seemingly then, the coastal station data should better reflect the environmental conditions that affect the fish. However, the coastal station data were taken near a river estuary and thus also may have not reflected the actual temperatures that the fish experienced. For these reasons, two different models were examined: one using LNCPUE, SAL5M and average SST, and one using LNCPUE, SAL5M and SST5M.

We model the dynamics by identifying and estimating a vector ARMA model of the form (2). We simultaneously model LNCPUE and the environmental variables. This is especially important for our data as SST and salinity tend to be highly intercorrelated. To identify the proper form of the model (AR, MA, or ARMA) and the appropriate lags to be included in the model, we examined the cross-correlation matrices and the generalized partial-correlations (Tiao and Box 1981). The autocorrelation functions of SST and SST5M showed a strong annual seasonal cycle, while that of SAL5M showed a 6-mo cycle with perhaps a smaller annual seasonal term. The autocorrelation function of LNCPUE did not suggest a seasonal cycle; there were significant peaks around lags of 1, 6, and 12 fortnights.

The cross-correlation functions between LNCPUE with SST or SST5M showed persistent significant correlations at lags of roughly five to 15 fortnights. The partial-correlations were significant at only a few lags both for LNCPUE with itself and with the environmental series. The decaying behavior of the cross-correlations coupled with the spikes in the partial-correlations suggested that an AR model was appropriate (Tiao and Box 1981).

The lags suggested by the partial-correlations were then used in an exact maximum likelihood routine (Tiao et al. 1980) to estimate the AR parameters. Nonsignificant parameters were then removed from the models, and any additional parameters suggested by the residual covariance matrices were added to the models. In general, the model using SST5M tended to give both a better overall fit to the data as well as better behaved residual series. For this reason, we will concentrate on this model only. The estimated parameters to model LNCPUE are (see Table 2 for the complete model):

$$\begin{aligned}\text{LNCPUE}(t) = {} & 0.304*\text{LNCPUE}(t-1) + 0.144*\text{LNCPUE}(t-2)\\ & + 0.191*\text{LNCPUE}(t-6) - 0.057*\text{SST5 M}(2t-1)\\ & - 0.078*\text{SST5M}(t-5) - 0.062*\text{SST5M}(t-13)\\ & + 0.028*\text{SAL5M}(t-1) - 0.098*\text{SAL5M}(t-4)\\ & + 0.120*\text{SAL5M}(t-5) - 0.073*\text{SAL5M}(t-6).\end{aligned}$$

The residual cross-correlation matrices showed no lack of fit for this model, and the normalized residuals appeared to satisfy most of the Gaussian assumptions of the model. The model using SST5M explained 33% of the variance in LNCPUE. The model does a particularly good job at predicting the large peaks in LNCPUE.

Improving the Model Predictions

There are a priori reasons to believe that the relationships between CPUE and the environment are nonlinear or discontinuous in nature. For example, there is most likely a maximum temperature beyond which the fish are not found in abundance; a further increase in the temperature will not change the number of fish. Likewise, there probably is a minimum temperature below which the fish are not found; a further decrease in temperature will have no additional effect. Marchal (1967) notes that outside the optimum ranges for temperature or salinity the relationships may be very different in form than within the optimum ranges.

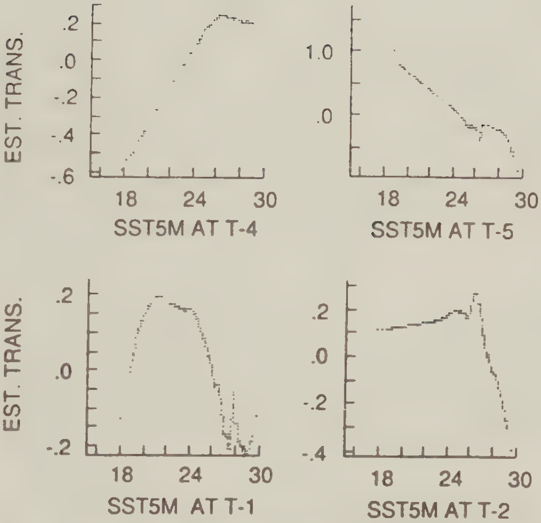


FIG. 4. Estimated optimal transformations of SST5M for predicting spatially aggregated CPUE.

The models we have estimated so far are all linear. To obtain a more realistic model, we used a technique due to Breiman and Friedman (1985) that calculates optimal transformations for a given dependent variable and a set of predictor variables, while preserving an additive structure to the model.

It is necessary to reidentify the proper model (i.e. what variables and what lags to use as predictors) for the transformed case, as it is possible that if the optimal transformations were known a priori, then variables that were not important predictors on a linear scale might become important predictors on the transformed scale. To this end, predictor variables to be included in the final model were selected by a stepwise procedure. First, all lag one variables were included in the model, entered in order of CPUE, SST5M, and SAL5M. (Some studies have shown that the order of the variables affects the transformations. We always enter CPUE first, so that any bias is conservative for environmental effects.) Any variable that was essentially transformed into a constant was removed.

Then models with lags 1 and 2, lags 1,2,3, etc. were used in the transformation algorithm, up to a lag of 15 fortnights. If the addition of the three variables in a new lag did not decrease the residual variance to a significant degree, then the entire lag was not included in the model. This stepwise procedure is highly nonoptimal and may well select a set of variables whose transformations do not explain as much variance as some other set of variables. Surprisingly, we ended up with a model very similar to the linear model in terms of the variables included in the model. However, the form and interpretation of the model differed substantially from the linear AR model.

The transformed model explained 55% of the variance of the transformed CPUE, a substantial increase over our original

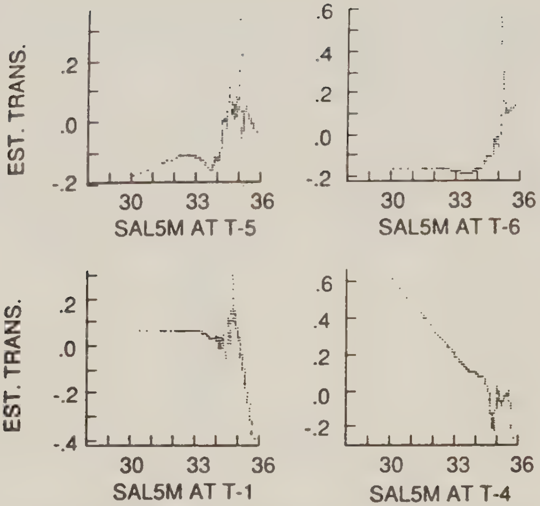


FIG. 5. Estimated optimal transformations of SAL5M for predicting spatially aggregated CPUE.

model. The transformations for CPUE at time *t* and at a lag of one fortnight are both very close to the natural log transformation selected a priori in our original models (Fig. 3). The estimated transformation for SST5M displays behavior consistent with our a priori reasoning (Fig. 4).

There is an increase in value between 18 and 20°C, a nearly constant value to 24°C, a sharp drop to 27.5°C, and a small rise to 28°C before dropping again. This suggests that at one period previous, conditions are most favorable between 20 and 24°C, dropping off sharply if the water is either colder or warmer. The small rise around 28°C may be water that is at the boundary of a frontal structure (Bakun 1978).

The estimated transformation for SST5M two fortnights earlier (Fig. 4) suggests that there is a slight preference for temperatures between 27–28°C, but mainly that temperatures greater than 28°C are not desirable. At four fortnights previous, the transformation of SST5M is linear with an asymptote around 26°C, while at five fortnights earlier the transformation is nearly linear with a preference for colder waters.

The transformation of SAL5M at one fortnight earlier (Fig. 5) suggests a preference for salinity at 35‰, with a strong avoidance of any greater density. The period from six to four fortnights prior shows a preference for a density in a narrow band centered at 35‰ at both six and five fortnights earlier, followed by a transition to relatively low densities of salinity. If this occurs at the same time that colder water is being replaced by warmer water, then CPUE should be particularly high.

Forecasting

The parameters for the linear model using LNCPUE, SST5M, and SAL5M were reestimated using data only from the years 1966–80. The new parameter estimates were close to the old ones, with no significant difference in the form of the estimated model. These parameter estimates were then used to calculate one-step ahead forecasts of CPUE, i.e., forecasts that assumed that at the start of each fortnight the data from the last fortnight were available. This would be equivalent to a real-time forecasting system.

The forecasts were transformed back to the original scale using the unbiased inverse transform (Granger and Newbold 1977):

$$(8)\quad \mathrm{CPUE}(t)=\mathrm{EXP}(\mathrm{LNCPUE}(t)+0.5*(\mathrm{SE}**\ 2\ )),$$

where SE is the standard error of the forecast on the transformed scale. The forecasted values for 1981 and 1982 (Fig. 6) describe quite well the increase of CPUE during the main upwelling season which began in fortnight 13 in 1981 and fortnight 14 in 1982. The model does not forecast as well during other parts of the year.

Implications of the Analysis

It is not surprising that our linear model explains only 33% of the variance in CPUE of *S. maderensis* and predicts only broad changes in CPUE. This is a multispecies fishery that is not targeted on any one species. There does not appear to be a good way to partition effort between the species, and thus our measure of CPUE is highly biased and may only roughly reflect availability or abundance of *S. maderensis*. A single species that is more coastal in its distribution is more likely to have different environmental features dominate its dynamics during different times of the year. That is, the problem is nonstationary while we have restricted ourselves to stationary models.

Nevertheless, our model has a biological interpretation that is consistent with previous studies, and the differences between this model and our previous model for all species combined (Mendelssohn and Cury 1987) reflect known differences between *S. maderensis* and most of the other species. Moreover, the improvement in fit when transformations were calculated suggests that much of the relationship with the environment is nonlinear and only roughly approximated by a linear model.

Mendelssohn (1990) examines the affects of the optimal transformations in the frequency domain, both for the combined species model and for the models of *S. maderensis* only. For the combined species, LNCPUE, as compared with CPUE, shifts the spectral peak from a period of approximately 1 mo to a peak centered at a period of 5 wk. The estimated transformations for SST5M and SAL5M also shift the spectral peaks to the same frequency band, thus aligning the spectral peaks in all three series.

Both transformed SST5M and transformed SAL5M are strongly coherent with LNCPUE for the combined species at this frequency band, but partial coherences (the frequency domain equivalent to partial correlations) show that only transformed SST5M is important. The coherence between LNCPUE with transformed SAL5M is due to the coherence between transformed SST5M and transformed SAL5M.

For *S. maderensis* only, Mendelssohn (1990) shows that while the coherences between LNCPUE for *S. maderensis* with transformed SST5M and transformed SAL5M are significant at the same frequency bands, the partial coherences are significant at different time scales. Transformed SST5M shows significant partial coherences at lower frequencies, while transformed SAL5M has significant partial coherences at higher frequencies.

Our analysis of CPUE for all species combined revealed no relationship with salinity (Mendelssohn and Cury 1987). Our present models, particularly after the transformations, indicate that salinity is a crucial variable in predicting the CPUE of *S. maderensis*. In addition, a coastal measure of SST5M provided a better fit than a more offshore measure of SST. This is con-

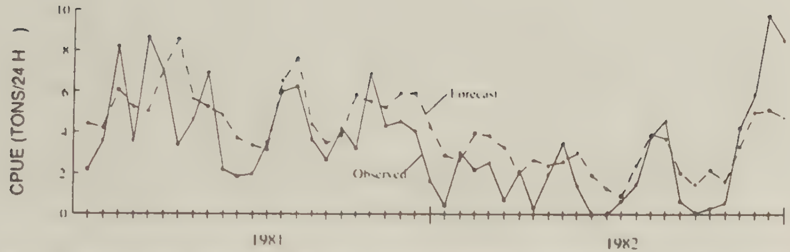


FIG. 6. One-step ahead forecast of CPUE for 1981–82 when only data through 1980 used to estimate the model.

sistent with the known fact that *S. maderensis* is a highly coastal species that is sensitive to salinity (FAO 1974). CPUE is predicted by CPUE lagged one, two, and six fortnights. The lags of one and two fortnights suggest that CPUE for *S. maderensis* is persistent. The lag at six fortnights may reflect environmental conditions occuring at that lag. Picaut (1983) shows that SST in the area has a spectral peak around a frequency of 45 d. The environment side of our model also suggests important behavior at this lag.

The lags of SST5M and SAL5M in the model, while open to interpretation, are not as immediately obvious. The model says that higher levels of CPUE will be found when starting six fortnights earlier, the waters make a transition from cooler, high-salinity waters to warmer, low salinity waters. This interpretation is strengthened by the estimated transformations, which show quite sharply the transitions from one type of water to another around four fortnights previous if CPUE is to be high. Why should a transition in the waters so much before the period of fishing affect CPUE so much? One possible answer is that at the beginning of the rainy season sudden and strong storms occur which decrease the salinity of the water. Upwelling usually starts about four fortnights later. The river outflows during this period bring terrigenous materials to the sea, and through a series of links, this improves the zooplankton productivity in the area (Binet 1976, 1983), the food of that species (Dia 1972). We emphasize that while this explanation has events occurring in the proper sequence, so might other explanations. Our model does not validate this explanation.

While a number of assumptions have been made, it appears that the enrichment in the food, which is triggered by environmental changes, plays an important role in the observed fluctuations in CPUE for *S. maderensis*. While the fish may be sensitive to salinity levels, salinity and temperature variables appear to reflect more a dynamic process that creates the proper conditions for the fish, rather than absolute measures of the conditions that are favorable to the fish. That the dynamics of the dominant species, *S. maderensis*, differs to a great extent from the dynamics of the combined species suggests that it may be preferable to aggregate forecasts of individual species rather than to forecast the aggregate behavior.

Space–Time Models

The general pattern of the seasonal migration for *S. aurita* off the Ivory Coast and Ghana has been described in ORSTOM/FRU (1976), and Binet (1983) has analysed the similarities between the migratory pattern of *S. aurita* and the spatial dynamics of zooplankton in the same area. For *S. madernesis*, Marchal (1967) briefly speculates on possible migratory patterns between the areas, but otherwise not much is known of the migratory behavior of *S. maderensis*. Since environmental factors play an important role in the migrations of *S. aurita* we expect that the same may be true for the migrations of *S. maderensis* off the Ivory Coast. In this section we analyze the fluctuations in the CPUE and environmental time series across areas to clarify the patterns of migration and their possible linkages with climatic factors.

The spatially disaggregated CPUE series (Fig. 7) were modeled with area specific SST as the environmental series (Fig. 8), making a simultaneous model with eight series in total. The results of the previous section suggest that a more coastal measure of temperature would be preferable, as well as an area specific measure of the salinity of the water. However, these series were only available from the one coastal station.

For an initial analysis of the data we used a subset autoregression procedure due to Akaike et al. (1979) with a maximum allowable lag of 12 fortnights to construct a simultaneous model of the eight series. (Hereafter, SST4 will denote SST in area 4, CPUE4 will denote CPUE in area 4 etc.) The results of the subset autoregression (Table 3) were mixed. While the parameters for the model did seem to indicate a migratory pattern (discussed below) the fit to the data is quite low with an r-squared no better than .15 in any of the areas.

Due to the lack of fit in the space–time model, optimal transformations were calculated to predict the CPUE in each area using the same stepwise selection process as in the previous section. The variables were always entered lower order lags before higher order lags and CPUE series before SST series.

The transformations greatly increased the predictability of the transformed CPUEs, with r-squared values of .47, .50, .58, and .53 for areas 4,5,6, and 7, respectively. For each area, lags of one, two, and four fortnights were found to be important in predicting CPUE for that area. The migratory pattern suggested by the transformed series qualitatively was the same as suggested by the linear AR model. We will discuss the suggested migratory pattern and then examine the transformations in areas 4 and 7 more closely.

Migration

The transformed variables suggest that migration between areas is associated with higher or lower levels of CPUE in given areas during the preceding periods as well as the relative temperature of the water in each area and its movement between areas during the preceding time periods.

The overall pattern suggested by the transformed model (Figs. 9 and 10) is that areas 6 and 7 vary together, area 4 varies separately from the other areas, and area 5 is a transition zone. A major fishing area is located in area 7 but often overlaps into

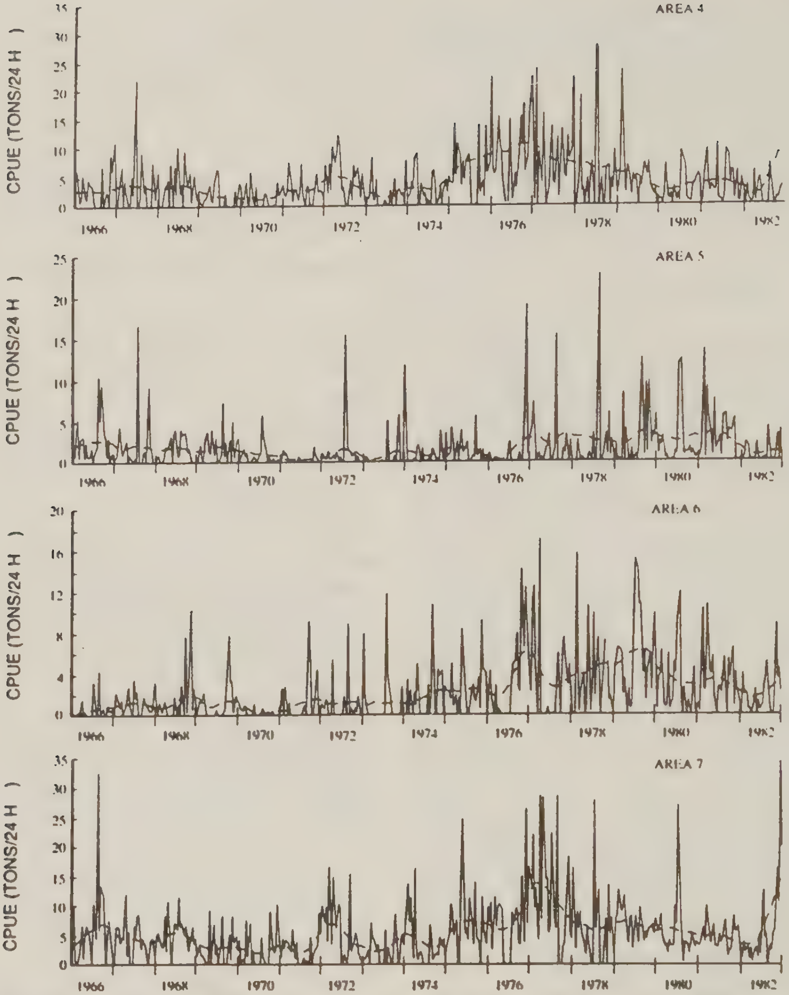


FIG. 7. Filled-in series of CPUE for *S. maderensis* by area. Solid lines are the data series while dashed lines are estimated local trend lines.

area 6. This probably explains why these two areas vary together.

In more detail, from the figures an east–west migration clearly appears in CPUE as shown in the one and two fortnight lags between areas 4 and 7. A reverse movement in CPUE is shown in the lags of one and four fortnights with area 4, indicated by the eastward pointing arrows in the figure.

A very similar pattern is seen for transformed SST (Fig. 10). An east–west migration, particularly from area 4 to areas 6 and 7 is seen, and at the same lags as with CPUE. A similar return migration is also seen, though the relationship with area 6 is not as clear as with CPUE.

The transformed SST suggests that CPUE4 is usually higher when area 6 and area 7 have environmental conditions that are associated with lower values of CPUE6 and CPUE7. Combining these observations, we suggest that the proposed migratory pattern may be due to the fish moving to the areas with the most favorable environmental conditions. The transformed SST (discussed below) appear to associate favorable conditions with frontal structure. The west-to-east movement probably reflects advection due to the Guinea Current while the east-to-west movement, reflects changes in upwelling (Bakum 1978; Picaut 1983).

Optimal Transformations

The main fishing areas are located in areas 4 and 7. Therefore we will only examine in detail the transformations for these two areas. The estimated transformation for CPUE7 (not shown) is very close to the log transformation that we have used throughout this paper for a priori reasons. The transformation of CPUE7 at time $t-1$ (not shown), however, suggests two regimes: a value of CPUE7 of 5 t per 24 h search or less and a value of CPUE7 of 10 t per 24 h search and greater. Generally, when CPUE7 has been high it tends to persist for two fortnights or longer at the high level. CPUE7 is generally higher when CPUE4 and CPUE6 were higher the previous fortnight. The

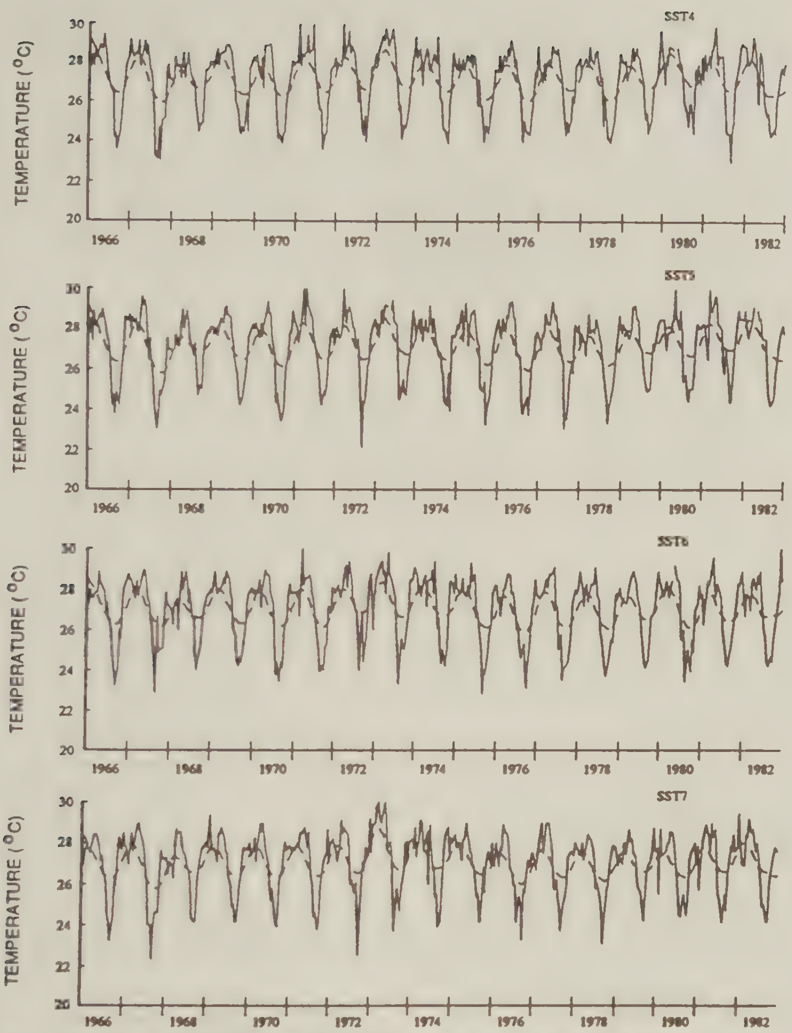


FIG. 8. Filled-in series of SST by area. Solid lines are the data series while dashed lines are estimated local trend lines.

transformations of CPUE at higher lags are similar in form, though they may be the inverse function.

The transformation of SST7 (Fig. 11) suggests three regimes: when the temperature is less than 24°C, when the temperature is between 24 and 28°C, and when the temperature is greater than 28°C. These values correspond with the isotherms used by Bakun (1978) to define the different oceanographic regimes in the area. Generally, CPUE7 is higher when SST7 two fortnights ago is less than 24°C, while SST7 one fortnight ago is greater than 25°C, preferably greater than 28°C. This suggests that the best fishing will occur in this area when there has been a transition in the water probably due to the passing through of a frontal structure.

A similar but not identical change in SST4 (Fig. 12) also leads to higher levels of CPUE7, though higher levels of CPUE4 occur when SST7 undergoes a change that causes lower levels of CPUE7. The transformed values of SST4 and SST7 one fortnight previous define to a large degree when there will be high levels of CPUE7 (greater than 10 t per 24 h search). If we plot SST4 one fortnight previous versus SST7 one fortnight previous and mark the points with high CPUE7 (not shown) the points with high CPUE7 show about the same distribution as the rest of the points. However, the same plot for the transformed variables (Fig. 13) shows that the points with a high CPUE7 are clustered in one region, to a large degree separated from the rest of the data.

The estimated transformations for area 4 (Figs. 14 and 15) have a similar interpretation. The transformation of the dependent variable CPUE4 (not shown) is also very close to a log transformation. Higher levels of CPUE4 will occur when SST4 makes a transition from colder waters two fortnights previous to warmer waters one fortnight previous (Fig. 14). At the same time SST7 should make a transition from warmer (but not too warm) to colder waters (Fig. 15).

TABLE 3. Model estimated by subset autoregression procedure due to Akaike for space–time model.

Lag		LNCPUE4	LNCPUE5	LNCPUE6	LNCPUE7	SST4	SST5	SST6	SST7
1	LNCPUE4	.115			.137				
	LNCPUE5	−.041	.109		.015				−.182
	LNCPUE6	.006	.023	.212	.021			−.151	.064
	LNCPUE7	.017	.020	.042	.226			.128	−0.13
2	LNCPUE4	.089		.132	.157				
	LNCPUE5	−.087	.212	.123			.135		
	LNCPUE6	−.007	.045	.140			.029		
	LNCPUE7	.003	.039	.070			.025	−.123	
3	LNCPUE4	.099							
	LNCPUE5	.011							
	LNCPUE6	.016		.103					
	LNCPUE7	.023		.021					
4	LNCPUE4								
	LNCPUE5								
	LNCPUE6				.086				
	LNCPUE7				.017				
Initial variance		1.177	.866	1.106	1.111				
Residual variance		1.051	.752	.881	.900				

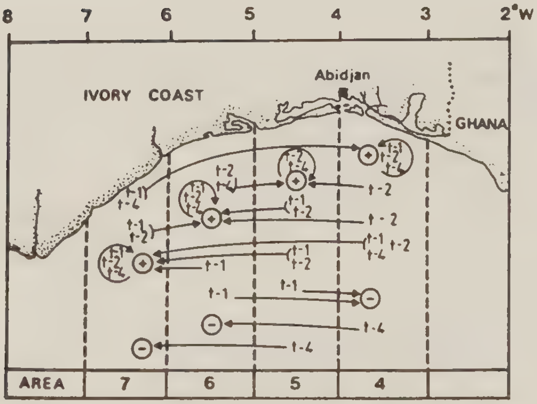


FIG. 9. Schematic representation of migration pattern in CPUE suggested by the transformed model. The plus or minus signs indicate the direction of the influence (higher or lower CPUE), the arrows show which areas affect other areas, and the time lags of the relationships are also shown.

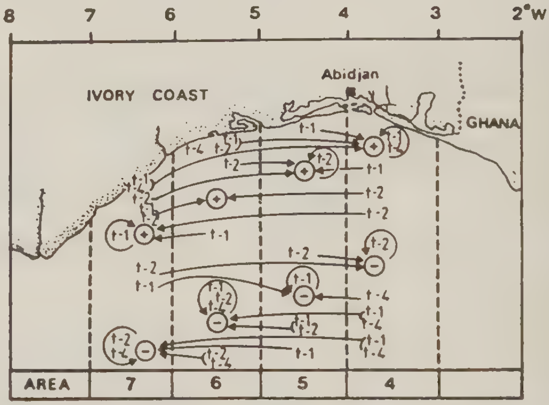


FIG. 10. Schematic representation of the propagation in SST suggested by the transformed model. The figure is interpreted as in Fig. 9.

Plots of transformed SST4 and SST7 through time (not shown) show that the ideal conditions in area 7 for high CPUE4 rarely occur at the same time as the ideal conditions in area 4. Thus CPUE4 tends to be higher either when conditions are favorable in area 4 but not too favorable in area 7 or when conditions are not unfavorable in area 4 but conditions in area 7 are very unfavorable. Unlike in area 7, SST4 and SST7 one fortnight previous are not sufficient to identify periods with high CPUE4. This suggests that the process in area 4 is more complicated, involving both what the fish are doing and more complicated behavior in the ocean.

Discussion and Conclusions

While there must be caution in making interpretations of our space–time analysis for reasons mentioned previously, the general pattern that emerges is that of a west-to-east migration followed by an east-to-west migration. The fish appear to migrate mainly between areas 7 and 4, perhaps avoiding the fishery in the central area by going too deep for the gear. Environmental processes, measured here by the dynamics in SST, appear to influence these migrations. Zooplankton are one of the major food sources for *S. maderensis*, and comparing this proposed migratory pattern with the dynamics of zooplankton in the same region provides a plausible rationale for the migration. During the main cold season there is a general enrichment of zooplankton with an eastern movement associated with the Guinea Current. The zooplankton then make a return migration to the west (area 7) around August, associated with an undercurrent (Binet 1976). During the warm season, the western part of the Ivoirian Gulf (area 7) is the area most favorable for zooplankton enrichment and fishing also usually is favorable during this period. Area 5 generally is the area poorest in zooplankton (Binet 1976) and also generally has the lowest levels in CPUE.

Fishermen in the area have observed a lack of fish in the central areas and an apparent rapid migration of fish from one area to another. It is difficult to compare two different biological processes, especially when the evidence is circumstantial, but there appears to be enough evidence to develop some ten-

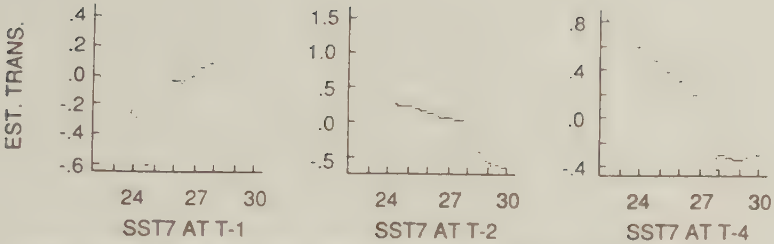


FIG. 11. Estimated optimal transformations of SST in area 7 for predicting CPUE in area 7.

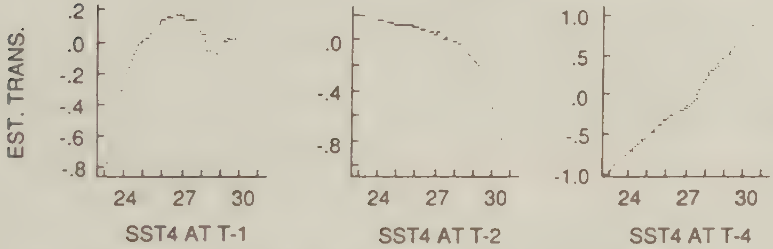


FIG. 12. Estimated optimal transformations of SST in area 4 for predicting CPUE in area 7.

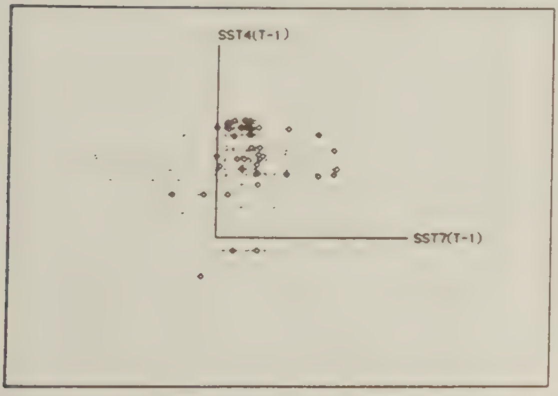


FIG. 13. Transformed SST7 versus transformed SST4. Diamonds mark time periods when CPUE in area 7 was high.

tative hypotheses and to point to the underlying environmental processes and fish behaviour that would have to be studied further to validate these hypotheses. The short (fortnight) time scales in which we find movement in the CPUE as well as the changes in the environment that lead to high levels of CPUE all seem to support the idea that the fish are migrating between areas where they can take advantage of sudden increases in zooplankton biomass caused by favorable environmental conditions (see Binet 1976). Further simultaneous studies of both zooplankton and *S. maderensis* in the same area would help to clarify some of these issues.

Our analysis has presented evidence that the dynamics of *S. maderensis*, both in space and time, appear to be influenced to a considerable degree by the environment. The space–time analysis suggests that the environment may be an indirect influence: favorable environmental conditions may be causing an increase in both the total biomass of the zooplankton as well as in the degree of aggregation of the zooplankton, as suggested by Binet (1976, 1983), and the fish move and take advantage of the increased biomass.

We have also shown that the relationships between CPUE and the environment most likely are highly nonlinear. If we are to better understand the dynamics, we must be careful to work on the appropriate functional scales. Simple linear methods will often obscure relationships that exist both in the data and in the real world. And finally, we have shown that the dynamics of an individual species, in this instance *S. maderensis*, can differ from the dynamics of the combined species of a fishery of which it is a part, both in terms of the behavior of the fish and in terms

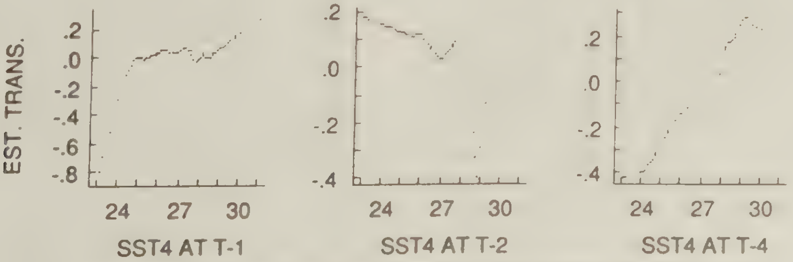


FIG. 14. Estimated optimal transformations of SST in area 4 for predicting CPUE in area 4.

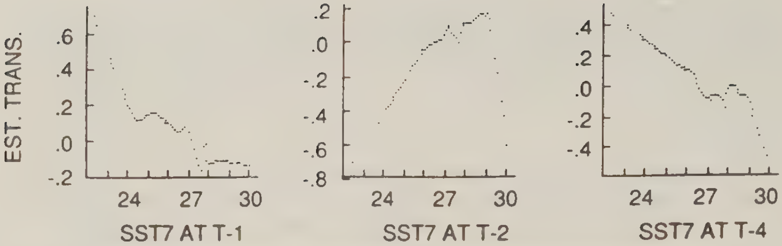


FIG. 15. Estimated optimal transformations of SST in area 7 for predicting CPUE in area 4.

of the oceanographic processes that influence the fish. Management based on the combined species dynamics could lead to unforseen changes in the dominant species. An open, but important question, is whether management plans or forecasts based on an aggregate of models for individual species would outperform models of the aggregate dynamics.

Acknowledgment

We wish to express out gratitude to the Centre de Recherche Océanographique d'Abidjan which made this study possible. Support for one of the authors (P. Cury) was provided through a cooperative agreement between NMFS and ORSTOM during a visit to the Pacific Fisheries Environmental Group, Monterey, CA. We thank Dr. I. Barrett and Dr. A. Bakun who made this visit possible.

References

AKAIKE, H., G. KITAGAWA, E. ARAHATA, AND F. TADA. 1979. TIMSAC-78, Computer science monographs. The Institute of Statistical Mathematics, Tokyo. 11. 279 p.

BAKUN, A. 1978. Guinea current upwelling. Nature (Lond.) 271: 147–150.

BAKUN, A., AND R. H. PARRISH. 1980. Environmental inputs to fishery population models for eastern boundary current regions. *In* G. D. Sharp [ed.] Workshop on the effects of environmental variation on the survival of larval pelagic fishes. IOC Workshop Rep. 28: 67–104.

BELVÈZE, H., AND K. ERZINI. 1983. The influence of hydroclimate factors on the availability of the sardine (*Sardina pilchardus* Walbaum) in the Moroccan Atlantic fishery. *In* G. D. Sharp and J. Csirke [ed.] Proceedings of the expert consultation to examine changes in abundance and species of neritic fish resources. Costa Rica, 18–29 April 1983. FAO Fish. Rep. 291 (2): 285–327.

BINET, D. 1976. Biovolumes et poids secs zooplanctoniques en relation avec le milieu pélagique au dessus du plateau ivoirien. Cah. ORSTOM, Sér. Océanogr. 14: 301–326.

1983. Zooplancton des regions côtières à upwellings saisonniers du Golfe de Guinée. Cah. ORSTOM, Sér. Océanogr. 18: 357–380.

BOUDREAULT, F. R., J. NORMAND DUPONT, ET C. SYLVAIN. 1977. Modelès linéaires de prédiction des débarquements de homard aux Iles-de-la-Madeleine (Golfe du Saint-Laurent). J. Fish. Res. Board Can. 34: 379–383.

BREIMAN, L., AND J. H. FRIEDMAN. 1985. Estimating optimal transformations for multiple regression and correlation. J. Am. Stat. Assoc. 80: 580–619.

CLEVELAND, W. S. 1979. Robust locally weighted regression and smoothing scatterplots. J. Am. Stat. Assoc. 74: 829–836.

CURY, P., AND C. ROY. 1987. Upwelling et pêche des espèces pélagiques côtières de Côte-d'Ivoire: une approche globale. Oceanologica Acta 10: 347–357.

DEMPSTER, A. P., N. M. LAIRD, AND D. B. RUBIN. 1977. Maximum likelihood from incomplete data via the EM algorithm. J. Roy. Stat. Soc., Ser. B. 39: 1–38.

DIA, A. E. K. 1972. Étude de la nutrition de certains clupéides de Côte D'Ivoire. Rapp. Sci. UNDP/SP/288/IV C6, Abidjan, RS/11/72.

FAO (FOOD AND AGRICULTURE ORGANIZATION). 1974. Rapport terminal du projet FI: DP/IVC/66/506: Étude et mise en valeur des resources en poissons pélagiques côtiers. Conclusions et recommendations. FAO, Rome: 72 p.

1982. Report of the *ad hoc* working group on the *Sardinella* off the coast of Ivory Coast–Ghana–Togo. Fishery Committee for the Eastern Central Atlantic CECAF/TECH/82/40 (En): 72 p.

FONTENEAU, A., AND E. G. MARCHAL. 1970. Récolte, stockage et traitement des données statistiques relatives à la pêche des sardiniers (filet tournant) en Côte D'Ivoire. Doc. Sci. C.R.O. Abidjan. 1: 21–30.

GRANGER, C. W. J., AND P. NEWBOLD. 1977. Forecasting economic time series. Economic theory and mathematical economics series. Academic Press, New York, NY. 333 p.

LAEVASTU, T., AND M. L. HAYES. 1981. Fisheries oceanography and ecology. Fishing News (Books) Ltd., Farnham, Surrey, England, 199 p.

MARCHAL, E. G. 1967. La pêche des sardiniers ivoiriens en 1966. Doc. Sci. Prov. C.R.O. Abidjan. 19: 26 p.

MARCHAL, E. G., AND J. PICAUT. 1977. Répartitions et abondance évaluées par échointégration des poissons du plateau ivoiro-ghanéen relation avec les upwellings locaux. J. Rech. Océanogr. Vol. 2 (4): 39–57.

MENDELSSOHN, R. 1990. Relating fisheries to the environment in the Gulf of Guinea: information, causality and long-term memory. *In* P. Cury [ed.] Impact des fluctuations climatiques sur les pêches pélagiques côtières en Afrique de L'Ouest. ORSTOM, Paris, France.

MENDELSSOHN, R., AND P. CURY. 1987. Forecasting a fortnightly abundance index of the Ivoirian coastal pelagic species and associated environmental conditions. Can. J. Fish. Aquat. Sci. 44: 408–421.

MENDELSSOHN, R., AND J. MENDO. 1987. Exploratory analysis of anchoveta recruitment off Peru and related environmental series, p. 294–306. *In* D. Pauly and I. Tsukayama [ed.] The Peruvian anchoveta and its upwelling ecosystem: three decades of change. Instituto del Mar del Pru (IMARPE), Callao, Peru; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.

MENDELSSOHN, R., AND C. ROY. 1986. Environmental influences on the French, Ivory Coast, Senegalese and Moroccan tuna catches in the gulf of Guinea, p. 170–188. *In* P. E. K. Symons, P. M. Miyake, and G. T. Sakagawa [ed.] Proceedings of the ICCAT Conference on the International Skipjack Year Program, ICCAT, Madrid.

MORLIÈRE, A. 1970. Les saisons marines devant Abidjan. Doc. Sci. C.R.O. Abidjan. 1: 1–15.

ORSTOM/FRU (OFFICE DE LA RECHERCHE SCIENTIFIQUE ET TECHNIQUE OUTRE-MER/FISHERIES RESEARCH UNIT). 1976. Rapport du groupe de travail sur la sardinelle (*S. aurita*) des côtes ivoiro-ghanéennes. Fishery Research Unit Tema, Centre de Recherches Océanographiques Abidjan, ORSTOM: 62 p.

PICAUT, J. 1983. Propagation of the seasonal upwelling in the eastern equatorial Atlantic. J. Physical Oceanogr. 13: 18–37.

SHUMWAY, R. H., AND D. S. STOFFER. 1982. An approach to time series smoothing and forecasting using the EM algorithm. J. Time Ser. Anal. 3(4): 253–264.

TIAO, G. C., AND G. E. P. BOX. 1981. Modeling multiple time series with applications. J. Am. Stat. Assoc. 76: 802–816.

TIAO, G. C., G. E. P. BOX, M. R. GRUPE, G. B. HUDAK, W. R. BELL, AND I. CHANG. 1980. The Wisconsin Multiple Time Series (WMTS-1) Program. A preliminary guide. Department of Statistics, University of Wisconsin, Madison, WI. 75 p.

8944

American Fisheries Society Symposium 6:66–82, 1989

Synthetic Estimates of Historical Abundance and Mortality for Northern Anchovy

RICHARD D. METHOT[1]

National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038, USA

Abstract.—The stock synthesis model combines the analyses of catch, abundance, and age-composition data. The model seeks the most likely time series of abundance and mortality, and distributes the residual error among all types of data according to each type's consistency with the synthetic estimates. The data base for northern anchovy *Engraulis mordax* includes two independent fisheries, an auxiliary source of age-composition data, a 6-year time series of accurate spawning biomass measurements by the egg-production method (EPM), and two longer time series of biomass indices. Specific biological relationships in the northern anchovy model are an influence of chub mackerel *Scomber japonicus* on natural mortality, and an influence of ocean temperature on patterns in age-specific availability and the fraction of 1-year-old fish that are mature. The synthetic estimates of spawning biomass since 1980 typically are within 15% of the measurements made by the EPM. This high precision demonstrates the consistency between changes in biomass measured by the EPM and changes expected from recruitment information in the age-composition data. Consistency between the other biomass indexes and age-composition data were lower. Nevertheless, the other biomass indexes are valuable for defining trends in the estimated 33-year time series.

Knowledge of the abundance of a harvested population is invaluable for an accurate assessment of the population's potential yield. Fishery-independent measurements of abundance are desirable, but precise estimates may be unavailable or prohibitively expensive. Much population assessment methodology involves the inference of abundance from fishery data. When fishery and survey data are available, we usually lack objective means of integrating them in a comprehensive analysis.

Separate virtual population analysis (VPA; Doubleday 1976) treats catch-at-age data, and was developed from the assumption that fishing mortality of each age-group in each year could be estimated as the product of an age-dependent availability to the fishery and an annual value for fishing effort. Separable VPA simultaneously analyzes all year classes in the fishery, resulting in a more determinate overall solution than conventional VPA (Murphy 1965); although the catch of each age in each year is no longer exactly reproduced by the model. Recent advances in catch-at-age analysis (Fournier and Archibald 1982; Deriso et al. 1985) include more careful attention to the error structure and establishment of a framework for inclusion of auxiliary information (fishing effort, survey estimates of age composition, stock-recruitment relationships).

The stock synthesis model (SS), like the models above, brings auxiliary data directly into the catch-at-age analysis. Synthesis of fishery and survey data into a coherent whole can provide a more accurate evaluation of the history and current status of the population. In this synthesis, the age-composition data describe year-to-year changes in relative abundance, whereas these data by themselves are inadequate for estimating trends or current abundance. Data from biomass surveys typically are too imprecise for estimating year-to-year changes in abundance, but they are invaluable for establishing the mean and trend. In its simultaneous examination of all data, the SS model distributes the residual error among the various types of data according to the specified level of confidence in each data type and the consistency of the data with the synthetic estimates.

The approach of the SS model is more similar to that of Fournier and Archibald (1982) than to that of Deriso et al. (1985) or to VPA. In the SS model, the numbers at age calculated by the deterministic population model are transformed to provide expected values for comparison to the varied data sources; the data are not manipulated into a number-at-age format. The user must be directly involved in specifying the relation between the model's estimates of numbers at age and the types of quantities that have been measured. Thus, it is a modeling approach, rather than a packaged model, that can be transferred to other species. Here, an application of the SS model to northern anchovy *Engraulis mordax* is described. Important aspects of this implementation are the breadth of the auxiliary information about northern anchovy and environmental effects on the species' age-specific availability.

---

[1] Present address: Alaska Fisheries Science Center, 7600 Sand Point Way NE, Building 4, Bin C15700, Seattle, Washington 98115, USA.

Deterministic Population Model

A deterministic description of a homogeneous, fished population with annual recruitment is as follows:

y is time (years, measured quarterly);
a is age (years, measured quarterly);
t is type (here, U.S. or Mexican fishery);
$P(y,a)$ is the age-specific abundance;

$$P(y+1,a+1) = P(y,a)e_{-Z(y,a)} \text{ is survivorship;} \quad (1)$$

$$P(y,0) = R(y) \text{ is the recruitment in year } y; \quad (2)$$

$$C(y,a,t) = P(y,a)\frac{F(y,a,t)}{Z(y,a)}\left[1\text{-}e^{-Z(y,a)}\right] \text{ is catch at age;} \quad (3)$$

$$Z(y,a) = M + \sum F(y,a,t) \text{ is total mortality;} \quad (4)$$

M is natural mortality;

$$F(y,a,t) = E(y,t)\,Q(a,t) \text{ is fishing mortality;} \quad (5)$$

$E(y,t)$ is nominal fishing effort;
$Q(a,t)$ is age-specific availability.

With estimates of M, $E(y,t)$, $Q(a,t)$, and $R(y)$, the above equations calculate $F(y,a,t)$, $P(y,a)$ and $C(y,a,t)$. The important questions are (1) How well do the estimated abundances, $P(y,a)$, and catches, $C(y,a,t)$, conform to data on the population and its fishery? and (2) How can we estimate values for the parameters defining M, $E(y,t)$, $Q(a,t)$, and $R(y)$ to maximize the likelihood of the available data base?

The important problem is that the data for northern anchovy, and for most other species, are not collected in the form $P(y,a)$ and $C(y,a,t)$. For example, northern anchovy abundance is measured as spawning biomass without age structure. Specification of the relationship between the estimated age-structured population, equations (1–5), and the available data base is critical for accurate estimation of the population's abundance and mortality. In addition, changes in observed age composition for northern anchovy (Mais 1981) indicate that M or Q or both changed during the late 1970s. The following sections first describe the data base for northern anchovy (Methot 1986), and then describe the incorporation of environmental effects on M and Q and the relationships between the estimated age-structured population and the expected values for quantities that can be compared to data collected for the northern anchovy.

Northern Anchovy Data

Abundance Observations

Three types of abundance observations are available for northern anchovy (Table 1). Spawning biomass measured by the egg-production method (EPM) is the quotient of two measured quantities: daily rate of egg appearance in the sea, and daily rate of egg production by mature females (Parker 1980). It is the most precise and accurate of available techniques (Bindman 1986), but has only been used during 1980–1985. Historical egg production (HEP) observations are the average abundances of newly spawned eggs during January–April (Lo 1985) and are available since 1951 (but triennial during 1966–1978). Here, the HEP is considered as an index of spawning biomass. Acoustic observations (sonar) of schooled northern anchovy abundance are available since 1969 (Mais 1974). None of these types of abundance observations are age structured, although measurements of age composition were made during the acoustic surveys.

Fishery

There are four components to the northern anchovy fishery: the reduction fishery in southern California, the reduction fishery in northern California, the bait and nonreduction fishery, and the reduction fishery in Ensenada, Baja California, Mexico. Age-composition data were available from the two largest components, the southern California and Mexican reduction fisheries. The fishery data described below were not expanded into a number-at-age format. The data were kept as catch biomass and, when available, age composition of the aged fish.

Prior to 1966, only annual harvest data were available from the U.S. fishery, and no age-composition data were collected (PFMC 1983; Methot 1986). Annual landings were split into 50%

TABLE 1.—Abundance of and auxiliary data for northern anchovy. The egg-production method (EPM) is a measurement of spawning biomass and the historical egg production (HEP) is the production of eggs during January–April as estimated by Lo (1985). Sonar is a measurement of schooled northern anchovy biomass made by the California Department of Fish and Game. The HEP and sonar observations are treated as indexes with arbitrary units. The biomass of chub mackerel *Scomber japonicus* influences the natural mortality of northern anchovy. Temperature was measured at the Scripps Institution of Oceanography pier, La Jolla, California, during January and February. The model was fitted to quarterly fishery data, not to the annual values presented here.

	Northern anchovy						
	Abundance			Fishery landings			
Year	EPM (10^3 tonnes)	HEP	Sonar	USA (10^3 tonnes)	Mexico (10^3 tonnes)	Chub mackerel (10^3 tonnes)	Temperature (°C)
1954		0.168		25.3		79	14.2
1955		0.316		25.8		77	13.2
1956		0.146		31.6		84	12.8
1957		0.364		22.1		52	14.6
1958		1.274		9.1		27	16.1
1959		0.992		7.6		59	15.6
1960		1.765		6.5		65	13.9
1961		0.653		8.9		104	14.6
1962		1.314		6.9		125	13.5
1963		2.275		6.1		87	14.4
1964		4.147		7.0	4.6	53	15.0
1965		4.019		8.3	9.2	18	13.3
1966		5.256		34.4	13.2	9	13.8
1967				36.5	20.1	5	14.0
1968				20.7	14.3	5	14.5
1969		3.821	438	66.3	3.9	5	14.3
1970			275	92.9	28.0	5	13.6
1971			233	46.5	20.1	5	13.1
1972		1.657	822	68.0	30.1	5	12.8
1973			1.671	126.0	15.4	5	15.0
1974			947	80.2	42.8	5	13.1
1975		19.691	3.086	149.4	55.0	10	13.2
1976				119.5	72.0	10	13.9
1977			1.984	107.5	142.0	97	16.0
1978		2.330	392	17.5	130.0	132	15.7
1979		5.426	292	53.2	198.0	292	13.9
1980	870	2.671	604	49.0	240.0	252	15.0
1981	635	4.376	567	56.2	258.7	333	14.6
1982	415		250	49.0	173.0	359	14.1
1983	652		532	8.5	87.0	244	15.9
1984	309	2.850	573	7.0	101.1	157	15.0
1985	521		1.015	5.3	118.8	457	13.8
1986						400	15.2

for the first semester and 50% for the second semester of the year, although data since 1966 show wide variation in the semester percentages. The weights at age for these early landings were assumed to be equal to the average weights at age in the U.S. fishery during 1966–1979 (Table 2).

The U.S. fishery data since 1966 were available as reduction harvest (PFMC 1983) and combined bait and nonreduction harvest (e.g., Thomson et al. 1985). These data were available as monthly or semesterly values, except annual landings of bait plus nonreduction fish for 1966–1978 were split into two semesters by the 40%:60% average partition for 1979–1984.

Age-composition and weight-at-age data from the U.S. northern anchovy reduction fishery are available in Methot (1986). These data were assumed to apply to the total harvest (reduction + nonreduction + bait) because the reduction fishery contributed about 90% of the total harvest. Only trivial numbers of age-0 fish occur in the U.S. fishery. Since 1966, the first- and second-quarter total U.S. harvests have been combined, as have the third- and fourth-quarter harvests.

TABLE 2.—Mean weight at age and fecundity of northern anchovy for all available years of data. Tabulated values were used in the model for years with no observations. "Total" categories include data from U.S. and Mexican waters.

	Age					
Quarter	0	1	2	3	4	≥5
U.S. fishery weight at age (g)						
2		12.9	17.5	21.0	24.5	28.8
4	11.2	16.6	19.4	21.8	24.4	26.3
Total survey weight at age (g)						
1		8.7	14.6	18.3	21.2	24.3
Total survey fecundity (eggs/g)						
1		2,464	4,867	7,599	9,030	9,030
Mexican fishery weight at age (g)						
2		11.2	13.4	15.0	16.5	18.6
3	8.5	12.5	14.4	16.0	17.6	18.6
4	8.2	12.8	14.6	18.1	19.2	18.6

This compression is reasonable because the reduction fishery is closed during July and August and has been closed during February and March since 1978. Age-composition data have ceased to be collected since 1983, when the fishery declined to a low level (Table 1).

Annual landings by the reduction fishery for northern anchovy in Ensenada, Baja California, were first recorded in 1962 (PFMC 1983; Methot 1986). Chavez et al. (1977) estimated age composition and catch by quarter in 1975 as the fishery increased (Table 1). Sunada and Silva (1980) provided age composition and catch for 1976 and 1977. Recent unpublished quarterly data were provided by Living Marine Resources, Inc. (Methot 1986). The first-quarter Mexican harvest typically was very small and was combined with the second-quarter harvest. Third-quarter age-composition data were not used because of variable availability of age-0 fish. Fish of age 4 and older contributed little to this fishery, and age-0 fish often dominated the fourth-quarter fishery.

Survey Age Composition

Midwater-trawl surveys of northern anchovy have been conducted by the California Department of Fish and Game nearly annually since 1966 and provide fishery-independent observations of age composition (Mais 1974; Parrish et al. 1985). Here, cruises were categorized into either a first-quarter (primarily February) or second-quarter (primarily April) period (Methot 1986). Also, separate age-composition estimates were made for U.S. and Mexican regions because most cruises were made only in U.S. waters, and younger fish tend to be relatively more common south of the USA–Mexico border. Surveys for which less than 100 fish were aged were not included in the SS analysis.

Northern Anchovy Model Specification

Equations (1–5) defined a deterministic description of an age-structured population and its fishery. This section describes a relaxation of the assumptions of constant natural mortality and availability, and the conversion of estimated numbers at age into expected values for quantities that can be compared to the four types of age-composition data and three types of abundance data.

Natural Mortality

Average instantaneous total mortality (Z) of northern anchovy, age 2 and older, during 1966–1980 has been estimated to be 0.97–1.09 per year (MacCall 1974; Hanan 1981). Hanan (1981) noted that total mortality has increased since 1977, and Mais (1981) noted that older fish are now rare in the population.

Gut contents of chub mackerel indicate that northern anchovy are commonly eaten by this predator. Chub mackerel abundance increased from less than 10,000 tonnes during 1966–1976 (Table 1) to more than 300,000 tonnes in 1985 (MacCall et al. 1985). It seems likely that natural mortality of northern anchovy has increased as a consequence of increased predation by chub mackerel, but the magnitude of this increase could not be estimated from available data. The SS model was used to explore likely magnitudes by defining natural mortality as

$$M = M_o + M_p \cdot \text{Pred.}$$

Pred is chub mackerel biomass on July 1, in 10^6 tonnes;

M_o is the natural mortality without chub mackerel;

M_p is the rate at which M increases with increasing chub mackerel biomass.

Investigated values of M_o were 0.4, 0.6, and 0.8. Investigated values of M_p were 0.0, 0.4, and 0.8.

Recruitment

Age-0 northern anchovy begin appearing in the Mexican fishery during July–September and sometimes dominate the Mexican fishery during the fourth quarter. Recruitment is defined to occur on July 1 at a nominal age of 0.5 years. The parameters that define the recruitments are independently estimated for each year. These recruitments are not constrained to follow any stock-recruitment relationship, and the SS model is not used as a technique for direct estimation of the stock-recruitment relationship. Recruitments and spawning-stock abundances estimated by the SS model can, however, be used to explore the relationship between parent stock, environment, and recruitment (Peterman et al. 1988).

Abundance

Biomass estimates were calculated on February 15 from estimated numbers at age at that time, observed body weight at age in the trawl survey for the first quarter of that year, and age-specific contributions (availabilities) to each type of survey. February 15 is consistent with the approximate mean date of the EPM and other first-quarter surveys. The expected values for the three biomass measurements are

$$B(y,t) = S(t)\sum_{a=1}^{A} Q(y,a,t)W(y,a)P(y,a);$$

A is 5 years and includes all older ages;

$B(y,t)$ is biomass in year y measured by technique t for $t = 5$–7 (5 = EPM, 6 = HEP, 7 = sonar), $t = 1$–4 specify age-composition data;

$W(y,a)$ is weight at age;

$P(y,a)$ is the number at age calculated by the model;

$Q(y,a,t)$ is age-specific availability;

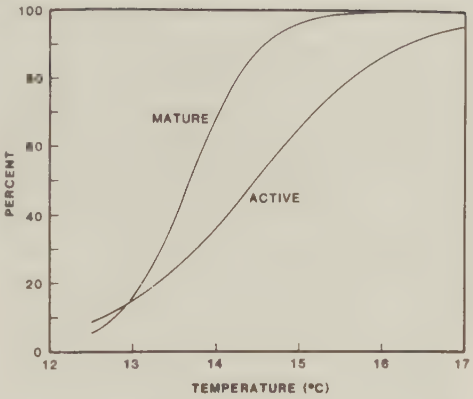


FIGURE 1.—Temperature effects on spawning by age-1 northern anchovy (Methot, unpublished data). Temperature is the mean temperature during January and February at the Scripps Institution of Oceanography pier, La Jolla, California. Mature northern anchovy are those with yolked eggs as disclosed by histological examination during 1979–1985. Active northern anchovy are those not classified as unsexable or immature by visual examination (Parrish et al. 1986) during 1966–1985.

$S(t)$ is a scaling factor: 1.0 for the calibrated EPM, and adjusted for the other data types to maintain a mean lognormal deviation of 1.0.

The abundance measurements are not age-structured, so the availability vector, Q, cannot reasonably be estimated within the model. For EPM and HEP, there is biological information that is used below to specify Q for those two types of abundance data. For sonar, Q is crudely estimated by the model.

The relation, $Q(y,a,5)$, between EPM spawning biomass and estimated age-specific abundance depends on the age-specific fraction of fish that are mature. Parrish et al. (1986) found that nearly all age-2 and older northern anchovy were mature during the major spawning season (January–April), and that the fraction mature was lower at age 1. Methot (unpublished data) found that the fraction of age-1 northern anchovy mature during late January–early March was related to temperature (Figure 1). Thus, the availability is 1.0 for ages 2 and older in all years, and the availability for age 1 is defined as

$$Q(y,1,5) = \frac{e^{A+BT(y)}}{1 + e^{A+BT(y)}};$$

$A = -33.40$; $B = 2.44$;

$T(y)$ is temperature at Scripps Institution pier during January and February.

The measured HEP values must be compared to quantities that are proportional to the estimated population's total egg production during January–April. Therefore, $Q(y,a,6)$ depends on the age-specific fraction of fish spawning and the age-specific fecundity of the spawners during this period. Methot (unpublished data) found that the temperature-specific fraction of age-1 female northern anchovy that were actively spawning during late winter was less than the fraction that were mature (Figure 1). Mean egg production by spawners during January–April was calculated from Parrish et al. (1986; Table 2). The availability, $Q(y,a,6)$, of spawners for HEP for ages 2 and older in all years is equal to the eggs per gram for that age because 100% of the fish are actively spawning. The availability for age 1 involves the fraction of fish active as well as fecundity:

$$Q(y,1,6) = \frac{e^{A+BT(y)}}{1 = e^{A+BT(y)}} \cdot 2{,}464;$$

$A = -17.51$; $B = 1.21$.

There is no information to define the availability to a sonar survey. Fish of ages 3 and older are assumed to be fully and equally available to the sonar survey. The availability at age 1, $Q(y,1,7)$, was assumed to be time-invariant and was defined as a parameter, AGE-1 SONAR, to be estimated by the model. Age-2 availability was the mean of the age-1 availability and 1.0.

Mean body weight at age was calculated from estimated mean length at age in first-quarter surveys and a length–weight relationship (PFMC 1983). In years without a sufficient sample to calculate mean body weight, the mean from other years was used (Table 2).

Deviations from expected biomass were calculated as

$$D(y,t) = \log_e \frac{\text{observed } B(y,t)}{\text{estimated } B(y,t)}.$$

The log-likelihood (l) for each type of abundance measurement is

$$l(t) = \frac{\sum_{y} -D(y,t)D(y,t)}{2\, s(t)^2} - n(t)\log_e s(t);$$

$s(t)$ is the standard deviation of the $D(y,t)$;

$n(t)$ is the number of observations of that type.

Magnitude of the Harvest

The total harvest is

$$H(y,t) = \sum_{a=0}^{A} W(y,a,t)C(y,a,t);$$

for the U.S. fishery $t = 1$, and for the Mexican fishery $t = 2$. The catches, $C(y,a,t)$, were calculated from equation (3), and the weights at age were observed or taken from Table 2. If there were measurements of the fishery's effort, the log-likelihood function would include deviations between the observed and estimated fishery efforts, and the $E(y,t)$ would be included in the vector of parameters to be estimated. Similarly, if there were constraints on permissable values for the $E(y,t)$, it would be appropriate to consider deviations between observed and estimated harvest. With northern anchovy, there are no measurements or constraints on the fishery effort, so the estimated $E(y,t)$ can be manipulated to match each $H(y,t)$ with the corresponding observed harvest. Consequently, the $E(y,t)$ were not included in the list of parameters to be estimated. As derivatives of the likelihood function are calculated for the other parameters, the efforts are constantly adjusted to match the magnitude of each observed harvest. Note that calculated survivorship (equation 1) depends on the model's current estimate of fishing mortality for a given age and year, not directly on the observed landings from that age and year.

Age-Specific Availability

There are four types (t) of age-composition data: U.S. fishery, Mexican fishery, U.S. survey, and Mexican survey (U.S. survey in Mexican waters). Age-specific availabilities, $Q(y,a,t)$, for each type were defined to follow the general form depicted in Figure 2 with parameters listed in Table 3. Three-parameter continuous functions were explored and judged too inflexible for the northern anchovy. Availability is defined as a function of time, y, to allow introduction of environmental effects. The estimated availabilities in each quarter and for each type of age composition were interpolated from the compound relationship (e.g., Figure 2), the actual age of the fish being measured in quarter years. For each type of age composition, the parameter AVAIL1(t) specified availability at age 1.0 in the first quarter for survey age composition and at age 1.25 in the second

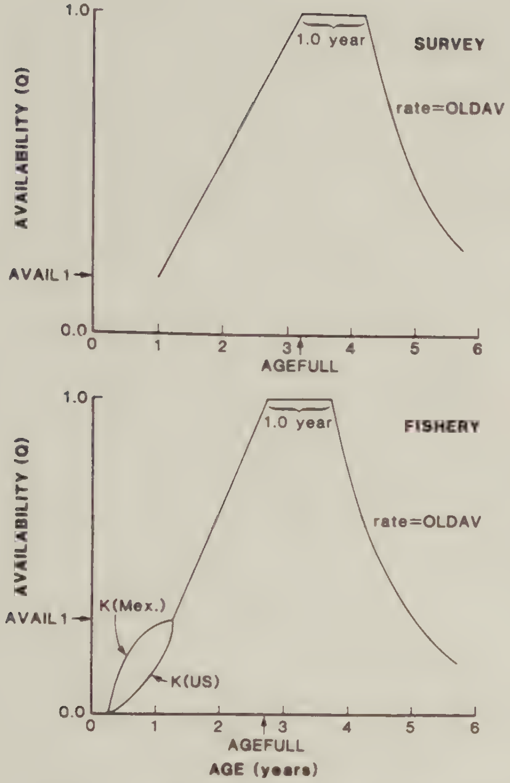


FIGURE 2.—Forms of age-specific availability functions for northern anchovy. The parameter AVAIL1 defines availability at age 1.0 (first quarter of year) for survey age composition, or at age 1.25 (second quarter) for fishery age composition. AVAIL1 can be more or less than 1.0. The parameter AGEFULL defines the age at which availability is 1.0. Availability remains at 1.0 for 1.0 year following AGEFULL, and availability of older fish declines at an exponential rate specified by the parameter OLDAV. K(Mex) and K(US) are parameters (for Mexican and U.S. fish) that define the rate at which availability increases from 0.0 at age 0.25 to AVAIL1 at age 1.25. AVAIL1 and AGEFULL are modified annually as a function of ocean temperature.

quarter for fishery age composition data. The parameter AGEFULL(t) specified the age at which availability was 1.0. Other parameters and environmental effects on AVAIL1 and AGEFULL are described below.

Young northern anchovy are less available to the U.S. fishery than to the Mexican fishery. The parameter $K(t)$ was introduced to specify the rate at which availability increased from 0.0 at age 0.25 to the estimated value AVAIL1(t) at age 1.25:

TABLE 3.—List of parameters included in the stock synthesis model for northern anchovy. Emphasis (user-specified) on the abundance data was set at 20. Common and availability parameters were estimated only from data and recruitments beginning in 1964. Pre-1964 recruitments and 1954 age composition were estimated with the common and availability parameters fixed at values shown here.

Parameter or age	Value	Year	Value
Common[a]		**Recruitment**[b,c] (number at age 0 on July 1)	
M_a	0.6		
M_p	0.4		
OLDAV	0.312	1954	0.070
SPRINGAV	0.503	1955	0.083
% MISAGED	0.310		
AGE-1 SONAR	0.237	1956	0.484
		1957	0.317
Availability[d]		1958	0.076
		1959	0.001
AVAIL1$_c$		1960	0.347
U.S. fishery	0.052		
Mexican fishery	0.264	1961	0.804
U.S. survey	0.010[e]	1962	0.985
Mexican survey	0.010[e]	1963	0.745
AGEFULL$_c$		1964	0.772
U.S. fishery	3.465	1965	0.268
Mexican fishery	3.142		
U.S. survey	3.860	1966	0.267
Mexican survey	3.199	1967	0.558
AVAIL1$_w$		1968	0.396
U.S. fishery	0.496	1969	0.662
Mexican fishery	0.921	1970	1.462
U.S. survey	0.341		
Mexican survey	1.366	1971	2.467
AGEFULL$_w$		1972	3.084
U.S. fishery	1.895	1973	2.297
Mexican fishery	2.116	1974	0.652
U.S. survey	2.484	1975	0.286
Mexican survey	1.999		
K		1976	1.143
U.S. fishery	3.955	1977	0.131
Mexican fishery	0.231	1978	2.285
		1979	1.639
Initial age composition (number on Jan. 1. 1954)		1980	1.480
		1981	0.393
Age 1	0.099	1982	1.835
2	0.024	1983	0.724
3	0.006	1984	1.839
4	0.003	1985	1.145
≥5	0.003		

---

[a] M_a = natural mortality in the absence of chub mackerel (fixed at 0.6); M_p = natural mortality in the presence of chub mackerel (fixed at 0.4); OLDAV = exponential decline in availability for ages greater than AGEFULL (age at which availability is 1.0) plus 1.0 year; SPRINGAV = adjustment for "excess" availability of fish older than AGEFULL during the second quarter of the year; % MISAGED = percentage of fish age 5 and older that were misaged by 1 year; AGE-1 SONAR = availability of age-1 fish to sonar surveys.

[b] Multiply by 50×10^9 to obtain absolute values.

[c] Not reliable prior to 1964 due to lack of age-composition data.

[d] AVAIL1$_c$ and AVAIL1$_w$ = cold- and warm-temperature availability of age-1 fish in the first quarter and of age-1.25 fish in the second quarter; AGEFULL$_c$ and AGEFULL$_w$ = age at which availability is 1.0 for cold and warm periods; K = rate at which availability increases from 0.0 at age 0.25 to AVAIL1 at age 1.25.

[e] Minimum permissible value.

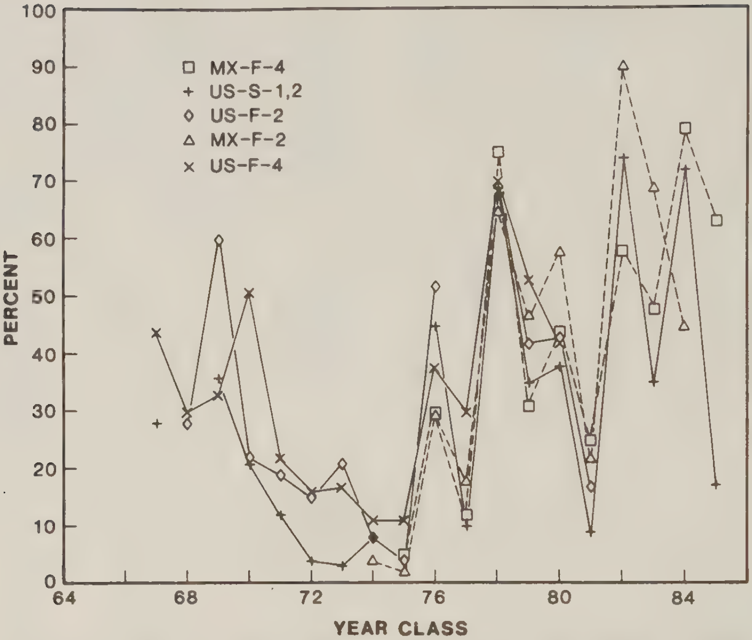


FIGURE 3.—Recruitment index for northern anchovy defined as the percentage of youngest fish in an age-composition observation. MX-F-4: percentage of age-0 fish in the fourth-quarter Mexican fishery (age = 0.75 years). US-S-1,2: percentage of age-1 fish in the first- or second-quarter trawl surveys conducted north of the USA–Mexico border (mean, if surveys were conducted in both quarters in same year). US-F-2: percentage of age-1 fish in the second-quarter U.S. reduction fishery. MX-F-2: percentage of age-1 fish in the second-quarter Mexican reduction fishery. US-F-4: percentage of age-1 fish in the fourth-quarter U.S. reduction fishery. The Mexican fishery trend is indicated with a dashed line to emphasize the temporal shift from entirely U.S. data to dominance by Mexican age-composition data. Data from the few surveys in Mexican waters are omitted for clarity. Age-0 fish in the fourth-quarter U.S. fishery are not presented because of their extremely low availability.

$$Q(y,0,t) = \text{AVAIL1}(t)(\text{age} - 0.25)^{K(t)};$$

age is age in years measured quarterly for ages less than 1.25.

Older northern anchovy have been underrepresented in the age-composition samples if one assumes constant mortality and availability. MacCall (1974) suggested that natural mortality increased for older northern anchovy, but such a trend is indistinguishable from decreased availability of these fish. Older northern anchovy tend to be found offshore and to the north (Parrish et al. 1985), so they certainly are less available to the Mexican fishery, and probably to the U.S. fishery as well. Reduced availability of older fish was modeled as an exponential decline for ages greater than AGEFULL(t) plus 1.0 year (Figure 2). The same exponential decline parameter, OLDAV, was used for all four types of age composition. When AGEFULL(t), the age at full availability, is greater than about 3.5 years, the OLDAV parameter has little effect on the expected age composition.

In the second quarter, the availability of older age-groups was greater than expected. This was especially apparent when there were U.S. trawl surveys in the first and second quarter of the same year. This phenomenon is probably due to some consistent, but undescribed, seasonal migration pattern. The model attempted to mimic this pattern by including a parameter, SPRINGAV, which was added to AGEFULL(t) in the second quarter.

The observed pattern of age-specific availability changed during the mid 1970s. In the early 1970s, the age-1 fish were highly unavailable to age-composition samples (Figure 3). Since 1976, and especially since autumn 1978, age-0 and age-1 fish became more common in the fishery and surveys

(Mais 1981), and ocean temperatures warmed (Table 1). Earlier surveys suggested that young fish were more common in southern California during warm periods (Baxter 1967). Such a shift in apparent availability could be due to a latitudinal gradient in stock structure. Off Mexico, size at age was smaller and young fish were more common (Parrish et al. 1985). During El Niño periods, the stock has shifted north, causing a decrease in size at age in southern California (Fiedler et al. 1986).

The above patterns suggest that availability can be modeled as a function of water temperature. A 4-year, linearly weighted average of temperature at the Scripps Institution of Oceanography pier during January and February (Table 1) was used as the temperature index $I(y)$. The current year had a weight of 4 and the value 4 years ago had a weight of 1. The temperature effect was imposed on the AVAIL1(t) and AGEFULL(t) by splitting each into a cold (c) and a warm (w) level (Table 3):

$$\mathrm{AVAIL1}(t) = \mathrm{AVAIL1}_c(t) \qquad \text{for } I(y) < I_{\min};$$

$$\mathrm{AVAIL1}(t) = \mathrm{AVAIL1}_c(t) + \frac{I(y) - I_{\min}}{I_{\max} - I_{\min}} \cdot [\mathrm{AVAIL1}_w(t) - \mathrm{AVAIL1}_c(t)] \quad \text{for } I_{\max} > I(y) > I_{\min};$$

$$\mathrm{AVAIL1}(t) = \mathrm{AVAIL1}_w(t) \qquad \text{for } I(y) > I_{\max};$$

$I_{\min}$ = 13.7°C (U.S. data types);
$I_{\min}$ = 14.2°C (Mexican data types);
$I_{\max}$ = 15.0°C.

The AGEFULL$_c$(t) and AGEFULL$_w$(t) were defined similarly.

Age-Determination Variability

Variance in age determination cannot be avoided and has the effect of smearing the sampled age composition as it becomes the observed age composition. A small misaging percentage, say 10%, has little effect on a good year class, but could double the apparent abundance of an adjacent small year class. In the SS model, the percentage of fish misaged into the adjacent age groups was assumed to increase linearly with age and to double from age 0 to the estimated value at ages of 5 and more. It was further assumed that no fish were misaged by more than 1 year. These estimated misaging percentages were used to adjust the estimated available age compositions before they were compared to the observed age compositions. Percentage misaged at ages 5 and more, %MISAGED, was estimated by the model.

Age-Composition Likelihood

Each of the four types of age-composition data was treated as a sample of the population's age composition, and a multinomial error structure was assumed (Fournier and Archibald 1982; Deriso et al. 1985). The probability of observing a particular sample age composition was expressed as the logarithm of the likelihood function.

$$D(y,t) = \sum_{a=0}^{A'} n(y,a,t) \cdot \log_e f(y,a,t);$$

$$l(t) = \sum_{y} D(y,t);$$

$n(y,a,t)$ is observed number of fish assigned to age a in a sample of type t collected during period y;
A' includes all older ages, and is the oldest age for which $n(y,A',t)$ is greater than five fish;
$f(y,a,t)$ is estimated proportion of fish of age a during period y in sample of type t.

The estimated age composition, $f(y,a,t)$, was calculated from the model's estimate of numbers at age during period y, $P(y,a)$; the age-specific availability to that type of sample, $Q(y,a,t)$; and estimated age-determination error.

Relative Emphasis on Data Types

The overall log-likelihood function, L, is a weighted sum of the log-likelihoods for each type of data (four age-composition types, three abundance types):

$$L = \sum_{t=1}^{7} \mathrm{EMPHASIS}(t) l(t).$$

EMPHASIS(t) is specified by the user.

The problem is quantification of confidence in the age-composition data relative to the abundance data. The objectivity with which the relative emphasis can be specified depends on the correctness of the error structure in the likelihood function. The multinomial formulation for error in age composition is incomplete because it deals only with the stochastic component of variation in age composition; inaccuracy in the age-specific availability functions is not explicitly modeled. Fournier and Archibald (1982) used a multinomial formulation, but recognized the problem of specifying the correct error structure. Deriso et al. (1985) evaluated the multinomial and two other error structures, and found that the selection mattered little to the end result. The SS model follows Fournier and Archibald by setting an arbitrary upper limit on the number of fish aged per time period. This de-emphasizes large age-composition samples, and prevents the model from attempting a perfect fit to these observations at the expense of other types of data. In recognition of the inherent subjectivity of the relative emphasis, the effect of increasing the relative emphasis on abundance data was explored.

Parameter Estimation

The complexity of the SS model for northern anchovy, and the philosophy which demands that the interface between model and data be tailored to each application, made application of standard statistical techniques, such as Marquardt's algorithm, impractical. Here, the search for the best parameter estimates depended on numerical evaluation of derivatives of the total log-likelihood function, L, instead of on derivatives of the expected values at each point in the data set.

The search for the best parameter values was based on quadratic hill climbing (Goldfeld and Quandt 1972), which is a modification of Newton's method, and included a Hessian matrix scaling described by Conway et al. 1970. The vectors of first (dX) and second (d^2X) derivatives of L with respect to each value of the parameter X were numerically evaluated in the region around the current estimates of the parameters ($\pm 5\%$ of X). The Hessian matrix, H, of mixed partial derivatives, which includes the d^2X on its main diagonal, also was calculated. The vectors of calculated parameter changes was calculated as follows.

DIAG_i = square root $-d^2X_i$ for each ith parameter;

$\mathrm{CORR}_{ij} = H_{ij}/[\mathrm{DIAG}_i\mathrm{DIAG}_j]$ for each ith, jth parameter;

$\mathrm{GRAD}_i = dX_i/\mathrm{DIAG}_i$ for each ith parameter;

$\mathrm{DEL} = \mathrm{CORR}^{-1}\mathrm{GRAD}$ (matrix algebra);

$\mathrm{DEL}_i = \mathrm{DEL}_i/\mathrm{DIAG}_i$ for each ith parameter;

The above calculations of the DEL_i are equivalent to $-dX_i/d^2X_i$ if all off-diagonal elements of H are zero. New parameter values were calculated by

$$X_{\mathrm{new}i} = X_{\mathrm{old}i} - \mathrm{DEL}_i.$$

In practice, when the X_{new} did not increase the total log likelihood L, the off-diagonal elements of CORR were multiplied by a fraction ($0.0 <$ fraction < 1.0) to emphasize the steepest ascent approach. Each evaluation of the overall log-likelihood function, L, takes about 3 s on an IBM PC/AT computer. Convergence of the complete model takes about 4 h, even if the numerous mixed partial derivatives are recalculated only when the absolute value of the previous estimate of CORR (i,j) was greater than a uniform random value (0–0.3). Second derivatives and large mixed partial derivatives typically changed less than 20% as the parameter vector moved towards convergence. Computation time and number of parameters would be much less for a model that did not include environmental effects on the availabilities.

There are two major classes of parameters (Table 3). One class includes all those parameters necessary to define the age-specific availabilities and environmental effects on these availabilities. The other set includes the recruitments for each year and the numbers at age in the first year of the time series. The fishing efforts are not included as parameters. Instead, they are constantly tuned; that is, efforts are adjusted so that estimated harvest equals observed harvest every time a parameter is tweaked to calculate a derivative and every time the parameters are changed as a result of the calculated derivatives.

The full model (recruitments and availabilities) was fitted to data from 1964 to 1986. This model was used to investigate the appropriate level of emphasis on abundance data and to define the availability functions. Then, with the availability parameters fixed, the model was run on data extending from 1954 to 1986 to estimate the full time series of abundance, recruitment, and fishing mortality.

Results and Discussion

Data Consistency

Before the SS model was fitted to data, the internal consistency of the age-composition and abundance data was investigated. An index of the information in the age-composition data is the percentage of fish in the youngest age-group (Figure 3). The incoming year class has been well represented in the fourth-quarter Mexican fishery at an age of about 9 months; a year class's percentage in that sample was highly correlated

TABLE 4.—Correlations among recruitment indexes (percentage at age 0 or 1) for northern anchovy during 1966–1985. Data sources are MX-F, Mexican fishery; US-F, U.S. fishery; US-S, U.S. trawl survey; MX-S, Mexican trawl survey. Mean percentages and correlations were calculated after values were transformed to arcsine square root; *N* observations is the number of years in which an age-composition observation was available for the indicated type and quarter.

	Data source and quarter of year								
Variable or source	MX-F 3	US-F 4	MX-F 4	US-S 1	MX-S 1	US-F 2	MX-F 2	US-S 2	US-F 4
Age (years)	0.5	0.75	0.75	1.00	1.00	1.25	1.25	1.25	1.75
N observations	9	15	11	15	5	14	9	8	14
Mean % at age	19.6	6.1	41.5	32.4	48.1	27.5	45.5	16.3	32.2
Correlations (decimals) and sample sizes (whole numbers)									
MX-F-3		0.89	0.65[a]	0.15[a]	0.73	0.70	0.05[a]	0.82	0.68
US-F-4	5		0.76	0.82	0.58	0.88	0.75	0.75	0.82
MX-F-4	9	7		0.72	0.82	0.89	0.62	0.99	0.92
US-S-1	8	10	10		0.95	0.93	0.80	0.85	0.81
MX-S-1	4	4	5	5		0.99	0.93		0.94
US-F-2	5	14	6	9	3		0.95	0.93	0.80
MX-F-2	7	6	8	8	5	5			0.92
US-S-2	3	7	3	5	1	7	2		0.93
US-F-4	4	13	6	10	3	12	5	8	

[a] Low correlation because of unusually high MX-F-3 values in 1984 and 1985.

with its percentage in other age-composition samples during the following year (Table 4). In contrast, the correlations among abundance data were not significant if the high HEP and sonar observation for 1975 were deleted (Table 5). These patterns of correlation among the age-composition and abundance data support the original goal: HEP and sonar data are best for constraining trends, and high-frequency variation in abundance must be inferred from the recruitment information in the age-composition data.

Fit to Biomass

The synthetic estimates of spawning biomass provided an excellent fit to the EPM spawning biomass observations (Figure 4). Varying the emphasis on abundance data affected the goodness of fit to EPM data (Table 6), but the general trend in spawning biomass was largely unaffected except for the early 1970s. With an emphasis of 20 on each of the three abundance data types, the root-mean-square lognormal error for EPM data was 0.175; that is, 95% of the EPM observations fell within 71 to 140% of the model's estimated values. This level of precision is satisfyingly close to the estimated coefficients of variation for EPM observations (0.15–0.20: Bindman 1986). This result suggests that application of the SS model has filtered out the small amount of measurement error in the EPM observa-

TABLE 5.—Correlations among three types of abundance data for northern anchovy. Sonar is an index of schooled biomass, HEP is an index of January–April egg production, and EPM is a measurement of spawning biomass by the egg-production method.

Comparison	*N*	*r*
EPM versus HEP	3	−0.003
EPM versus sonar	6	0.14
HEP versus sonar	8	0.94
HEP versus sonar[a]	7	−0.68

[a] The 1975 values were excluded.

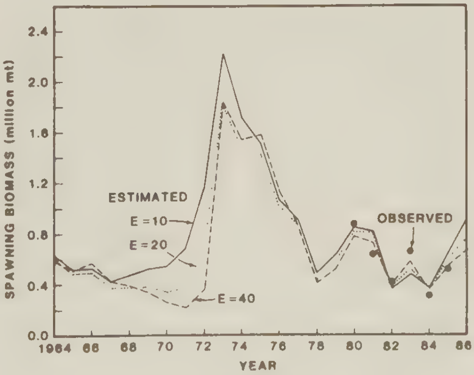


FIGURE 4.—Time series of estimated spawning biomass of northern anchovy. Measurements ("observed") of spawning biomass by the egg-production method (EPM) are represented by solid circles. Increasing the emphasis (E) on all abundance data during parameter estimation decreases deviations between observed and estimated EPM values; mt is tonnes.

TABLE 6.—Log likelihoods for the northern anchovy stock synthesis model as functions of the specified level of natural mortality (M_0), the chub mackerel influence on natural mortality (M_p), and the emphasis on the goodness of fit for abundance data (EMPHASIS). Goodnesses of fit to spawning biomass (EPM), egg-production index (HEP), and an index of schooled biomass (sonar) are first presented as the root mean square lognormal error (s) between the observed and predicted values. "All abundance data" are the sums of the log-likelihoods (L) for the three types of abundance data listed above. "All age composition" are the sums of the log likelihoods for the four types of age composition data. "All data" combines log-likelihoods for abundance and age-composition data after the abundance log-likelihood was multiplied by the emphasis factor.

	M_0 (upper) and M_p (lower)								
	0.4	0.4	0.4	0.6	0.6	0.6	0.8	0.8	0.8
EMPHASIS	0.0	0.4	0.8	0.0	0.4	0.8	0.0	0.4	0.8
Egg production method (s)									
1	0.48	0.42	0.36	0.36	0.33	0.33	0.29	0.29	0.33
10	0.28	0.27	0.26	0.22	0.22	0.23	0.20	0.21	0.23
20	0.23	0.22	0.20	0.19	0.18	0.19	0.17	0.16	0.17
40	0.20	0.19	0.17	0.16	0.12	0.10	0.09	0.07	0.06
Historical egg production (s)									
1	0.70	0.71	0.75	0.78	0.78	0.78	0.97	0.98	0.98
10	0.57	0.58	0.58	0.60	0.61	0.62	0.64	0.64	0.64
20	0.50	0.51	0.51	0.50	0.50	0.50	0.51	0.50	0.51
40	0.41	0.40	0.40	0.37	0.36	0.36	0.34	0.34	0.35
Sonar (s)									
1	0.62	0.65	0.67	0.86	0.86	0.86	1.11	1.13	1.16
10	0.54	0.54	0.56	0.61	0.63	0.64	0.70	0.71	0.71
20	0.50	0.50	0.51	0.51	0.52	0.53	0.58	0.57	0.59
40	0.46	0.45	0.45	0.45	0.45	0.45	0.45	0.46	0.47
All abundance data ($\log_e L$)									
1	1.1	0.5	0.4	−6.3	−5.8	−5.9	−19.9	−21.2	−23.3
10	8.8	8.7	8.4	7.5	6.9	6.4	5.1	4.4	3.6
20	12.5	12.7	12.8	13.7	13.4	12.8	11.9	12.5	11.1
40	16.8	17.7	18.6	19.9	21.8	22.9	23.9	24.3	24.3
All age-composition data ($\log_e L$)									
1	−98	−92	−90	−92	−90	−90	−99	−97	−97
10	−136	−133	−131	−151	−144	−141	−188	−182	−182
20	−190	−193	−197	−241	−240	−236	−287	−303	−297
40	−313	−336	−365	−416	−476	−502	−574	−595	−604
All data, with emphasis ($\log_e L$)									
1	−96	−91	−90	−99	−96	−96	−119	−119	−121
10	−48	−47	−47	−76	−76	−79	−138	−140	−149
20	60	60	59	34	28	19	−50	−53	−76
40	358	372	379	382	397	414	382	376	366

tions, and has resulted in an improved estimate of historical spawning biomass.

The trend in spawning biomass was rather insensitive to the level of natural mortality (Figure 5), and the goodness of fit to the EPM observations improved at higher levels of natural mortality (Table 6). This improved fit occurred because higher levels of natural mortality placed a larger fraction of the total biomass in the first age-group. This juvenation enabled the SS model to more easily track changes in observed EPM biomass by adjusting the estimated recruitment values. However, if the changes in observed EPM spawning biomass had not been basically consistent with the recruitment information in the age-composition data, the improved fit at higher levels of natural mortality could not have been realized without greatly degrading the fit to the age-composition data.

The variabilities of the HEP and sonar data were greater than that of the EPM data (Figures 6, 7) and increasing the emphasis on the abundance data did little to improve the fit to the observed HEP and

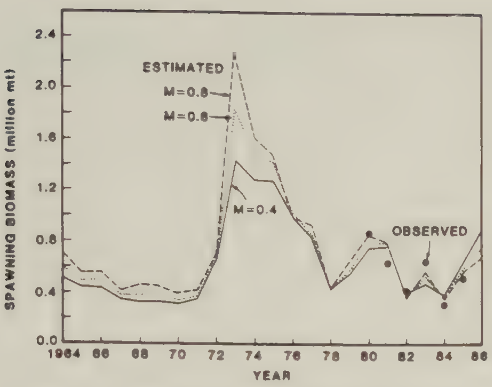


FIGURE 5.—Time series of estimated spawning biomass of northern anchovy, showing the effects of three levels of natural mortality (*M*). All three runs were made with an abundance emphasis of 20. Measurements ("observed") of spawning biomass by the egg-production method (EPM) are represented by solid circles; mt is tonnes.

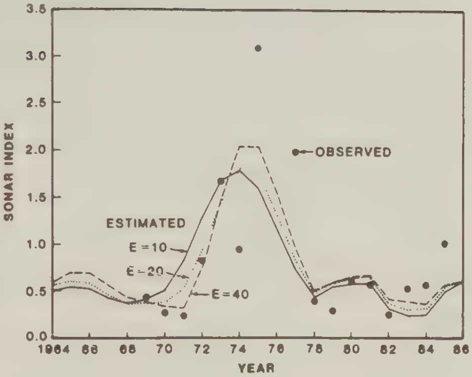


FIGURE 7.—Time series of the observed (solid circles) and estimated sonar index for northern anchovy. Increasing the emphasis (E) on all abundance data during parameter estimation decreases deviations between observed and estimated sonar values.

sonar data (Table 6). The estimated lognormal error of about 0.5 for HEP and sonar was greater than the average coefficient of variation (SE/mean = 0.42) calculated from the standard errors of each HEP observation (Lo 1985). This increase was expected because the former value includes structural and measurement error, and the latter value includes only measurement error.

Natural Mortality

A goal of the SS model was to estimate the natural mortality for northern anchovy and the contribution of predation by chub mackerel to this mortality. This goal was not realized because (1) the age-specific availability functions were sufficiently flexible to obtain a good fit to the observed age-composition data, regardless of the model's estimate of the true age composition; (2) different types of data were better fitted with high (or low) levels of natural mortality, so the level of emphasis on abundance data determined the "best" level of natural mortality (Table 6); and (3) the overall goodness of fit was insensitive to the level of chub mackerel mortality, probably because the increase in chub mackerel abundance was nearly coincident with the increase in temperature, which changed the shape of the availability functions, and with the increased Mexican fishery. Early attempts to estimate the mortality rates as parameters of the model were stymied by large mixed partial derivatives (i.e., high correlations) between the mortality parameters and some of the availability parameters.

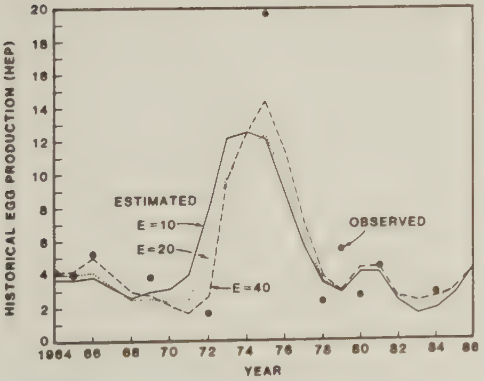


FIGURE 6.—Time series of observed and estimated historical egg production (HEP) by northern anchovy. Increasing the emphasis (E) on all abundance data during parameter estimation decreases deviations between observed (solid circles) and estimated HEP values.

The final version of the SS model had instantaneous natural mortality set at 0.6. This is less than the value of about 0.9 estimated by MacCall (1974), but larger values of *M* were highly inconsistent with the large abundance of old fish in 1975 and 1976. The effect of chub mackerel was set at a level, $0.4/10^6$ tonnes of chub mackerel, that increased natural mortality to 0.76 at the current abundance of chub mackerel (400,000 tonnes).

Availabilities and Aging Error

The SS model estimated that age-1 northern anchovy have been only 24% available to the sonar

TABLE 7.—Estimated age-specific availabilities for northern anchovy as a function of ocean temperature at the Scripps Institution pier. When the 4-year weighted temperature index, $I(y)$, was greater than 15.0°C or less than 13.7°C (14.2°C in Mexico) the indicated availabilities were used. At intermediate temperatures, availabilities were based on interpolated parameter values. The 20 parameters that define these availabilities are listed in Table 3; MX is Mexican.

		Age					
Data type	Temperature index (°C)	0	1	2	3	4	5
				First quarter			
US survey	13.7		0.010	0.356	0.702	1.00	0.849
	15.0		0.341	0.785	1.00	0.548	0.171
MX survey	14.2		0.010	0.460	0.911	1.00	0.393
	15.0		1.00	0.732	0.731	0.228	0.071
				Second quarter			
US fishery	13.7		0.052	0.401	0.749	1.00	0.720
	15.0		0.496	0.935	1.00	0.371	0.116
MX fishery	14.2		0.264	0.571	0.878	1.00	0.495
	15.0		0.921	0.979	1.00	0.479	0.150
US survey	13.7		0.084	0.378	0.672	0.967	1.00
	15.0		0.424	0.755	1.00	0.737	0.230
MX survey	14.2		0.102	0.468	0.834	1.00	0.528
	15.0		1.00	0.813	0.766	0.321	0.100
				Fourth quarter			
US fishery	13.7	0.003	0.266	0.694	1.00	0.717	0.224
	15.0	0.032	0.887	1.00	0.369	0.115	0.036
MX fishery	14.2	0.225	0.459	0.847	1.00	0.493	0.154
	15.0	0.785	0.966	1.00	0.478	0.149	0.046

surveys. This result depended primarily on the lag between the large recruitments in 1970 and 1978 and the respective low sonar observations in 1971 and 1979. No independent evidence for age-specific availability is known. Reduced availability of young fish may be due to the concentration of young fish in shallow water where the side-looking sonar is less effective, and to a lesser tendency for young fish to aggregate into detectable schools.

The SS model estimated that about 30% of older fish (≥5 years) were misaged under the assumption that the percentage misaged increased linearly with age and doubled from age 0 to age 5.

The patterns of availability to age-composition samples (Table 7) were defined by 20 estimated parameters: four parameters for each type of age composition and four common parameters (Table 3). As ocean temperature increased, young fish became more available to each type of age-composition sample.

Full Time Series: 1954–1986

Extension of the model to the beginning of the northern anchovy data base was hampered by the lack of age-composition data. Prior to 1964, the only data were U.S. fishery landings and the HEP index of spawning biomass. Running the model back to 1954 required the assumption that the temperature-specific availability to the U.S. fishery was the same during this early period as it was during the post-1964 period. The trend in estimated biomass prior to 1964 probably was accurately described by the model (Table 8). However, high-frequency variation in recruitments prior to about 1964 should not be considered reliable. Without other data, the model fit itself very well to the HEP observations, even though the post-1964 data indicated high variability in the HEP index. Thus, the good fit prior to 1964 is misleading, and the estimated high-frequency variation in recruitment must contain a large component due to the measurement error in the HEP index.

Fishing Mortality

Annual instantaneous fishing mortality (Table 8) has varied due to changes in the level of the fishery and the abundance of the estimated population. During 1954–1957, annual fishing mortality, F, of fish in fully available ages was high, ranging from 0.3 to 0.9. Two factors may have inflated estimated F during this period. Temperature was very cold, so few of the age-1 fish were contributing to the spawning biomass during the

TABLE 8.—Estimated biomass and recruitment of northern anchovy for the final stock synthesis model with emphasis of 20 on abundance data. Effort is the sum of the annual instantaneous fishing mortality rates, which were calculated quarterly (semesterly prior to 1966) then summed over the year for the values presented here.

Year	Biomass on Feb 15 (tonnes)		Recruitment[a] (in 10^9 fish)		Total fishery effort
	Total	Spawning	Jul 1	Feb 15	
1954	63,570	54,760	3.5	2.4	0.785
1955	53,610	37,920	4.2	2.6	0.869
1956	45,990	25,420	24.2	15.0	0.296
1957	153,920	141,160	15.9	10.8	0.474
1958	213,410	213,150	3.8	2.6	0.031
1959	182,370	182,160	<0.1	<0.1	0.027
1960	118,580	118,470	17.4	11.7	0.054
1961	170,820	160,900	40.2	26.9	0.073
1962	357,500	214,170	49.2	32.9	0.030
1963	563,040	520,210	37.3	25.1	0.012
1964	647,770	639,210	38.6	26.1	0.013
1965	695,280	531,520	13.4	9.1	0.024
1966	576,170	541,880	13.3	9.1	0.077
1967	434,270	409,170	27.9	18.8	0.127
1968	416.100	396.260	19.8	13.4	0.096
1969	395.650	374.300	33.1	22.6	0.168
1970	430.560	321,880	73.1	49.1	0.282
1971	678,390	333,600	123.3	83.9	0.131
1972	1,243,670	588,460	154.2	105.0	0.125
1973	1.848.680	1,812,900	114.9	78.6	0.094
1974	2,033,300	1,481,160	32.6	22.2	0.070
1975	1,606,570	1,458,430	14.3	9.7	0.118
1976	1,086,980	1,050,180	57.2	37.9	0.190
1977	870,170	868,890	6.5	3.8	0.387
1978	435,660	435,370	114.3	68.6	0.162
1979	869,270	582,890	82.0	46.3	0.209
1980	804,720	798,280	74.0	40.4	0.202
1981	814,930	782,770	19.7	9.5	0.422
1982	391,780	369,170	91.7	51.1	0.536
1983	552,200	534,590	36.2	21.4	0.157
1984	383,860	378,000	91.9	54.7	0.125
1985	767,490	589,060	57.3	34.0	0.096
1986	754,670	747,440			

[a] Recruitment estimates prior to 1964 are not based on any age-composition data, so they are much less precise than subsequent estimates.

early 1950s. If some of the age-2 fish were not spawning because of the cold temperatures, the total biomass would have been underestimated and the fishing mortality overestimated by the SS model. The second possibility is that age-0 fish were more available to the pre-1964 fishery than they were observed to be during the post-1964 period. If true, then the estimated fishing mortality rate necessary to obtain the observed landings would be reduced.

MacCall (1974) estimated that average *F* was 0.026 during 1964–1970, but this estimate was biased by the high biomass value (2.3×10^6 tonnes) used in his calculations. If his calculations are redone with the new estimate of average spawning biomass for this period, 460,000 tonnes, the average *F* for ages 2 and older is 0.128. The average annual *F* for fully available ages was estimated by the SS model to be 0.112 during the same period. Since 1975, the population has declined and the Mexican fishery has increased. Annual *F* in this period peaked at 0.54 in 1982.

Fit to Age Composition

Interannual variation in recruitment was estimated with high precision (Figure 8) because of the high consistency among the age-composition data sources and consistency with changes in EPM spawning biomass. However, the estimated recruitment index during 1970–1975 was consis-

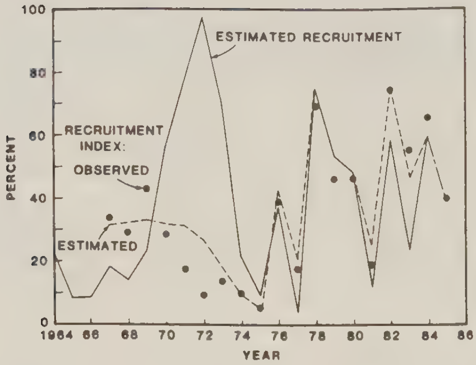


FIGURE 8.—Time series of estimated recruitment of northern anchovy, and the observed (solid circles) and estimated recruitment indexes. The observed recruitment index is the average of the recruitment indexes in Figure 2. The estimated recruitment index is the average of the estimates for which there was a corresponding observation.

tently larger than the observed index. There is no doubt that these year classes were abundant because of the large increase in biomass between 1972 and 1975 (indicated by HEP and sonar) and the high frequency of age-4 and older fish in 1975 and 1976. The discrepancy between the observed and estimated recruitment indexes for these years would have been greater were it not for the environmental effects built into the interface between estimated numbers at age and the expected values for the observations. The relation between temperature and the fraction of fish mature made the low 1972 HEP value more likely; the high egg production by older fish (Parrish et al. 1986) made the large HEP value in 1975 more likely; and the temperature effect on age-specific availability made the low recruitment indexes of these good year classes more likely. In addition, the recruitment index is a relative measure, so the first good recruitment masked the magnitude of subsequent good recruitments.

The above factors were not quite sufficient to resolve all of the discrepancy. The large abundance of old fish in 1975 could not be achieved without slightly overestimating the recruitment index in 1971 and 1972 (Figure 8) and overestimating the abundance observations during the same period. At higher levels of natural mortality, this discrepancy was exaggerated because recruitments during the early 1970s had to be even greater to make a large contribution to the biomass and age composition in 1975. The level of emphasis placed on the abundance observations critically determined the absolute level of spawning biomass during the early 1970s. Levels ranging from 1×10^6 to 3×10^6 tonnes were easily obtained (Figure 4).

The unresolved discrepancy between abundance and age-composition data during the early 1970s is not a problem with the SS model; rather, the model identified a shortcoming in our knowledge of northern anchovy. A plausible scenario is that the total biomass actually was large during the early 1970s and that age 1 *and age 2* northern anchovy were not spawning in 1972, which was a very cold year. Preliminary examination of the fraction of fish mature in samples taken from the reduction fishery indicates that only about 50% of the age-2 northern anchovy were spawning in 1972 (Methot, unpublished data).

The stock synthesis model is a flexible tool that has enabled a comprehensive review of historical abundance and mortality of northern anchovy. Patterns in deviations indicate shortcomings in our knowledge and identify areas for future investigation. For the present, the stock synthesis model is a valuable management tool because it provides a framework in which diverse types of data can contribute to current stock assessment.

References

Baxter, J. L. 1967. Summary of biological information on the northern anchovy, *Engraulis mordax*, Girard. California Cooperative Oceanic Fisheries Investigations Reports 11:110–116.

Bindman, A. 1986. The 1985 spawning biomass of the northern anchovy. California Cooperative Oceanic Fisheries Investigations Reports 27:16–24.

Chavez, H., S. Silva, and J. S. Sunada. 1977. The fishery for northern anchovy, *Engraulis mordax*, off California and Baja California in 1975. California Cooperative Oceanic Fisheries Investigations Reports 19:147–165.

Conway, G. R., N. R. Glass, and J. C. Wilcox. 1970. Fitting nonlinear models to biological data by Marquardt's algorithm. Ecology 51:503–507.

Deriso, R. B., T. J. Quinn II, and P. R. Neal. 1985. Catch-age analysis with auxiliary information. Canadian Journal of Fisheries and Aquatic Sciences 42:815–824.

Doubleday, W. G. 1976. A least squares approach to analysing catch at age data. International Commission for the Northwest Atlantic Fisheries Research Bulletin 12:68–81.

Fiedler, P. C., R. D. Methot, and R. P. Hewitt. 1986. Effects of California El Niño 1982–1984 on the northern anchovy. Journal of Marine Research 44:317–338.

Fournier, D., and C. P. Archibald. 1982. A general theory for analyzing catch at age data. Canadian Journal of Fisheries and Aquatic Sciences 39:1195–1207.

Hanan, D. 1981. Update of the estimated mortality rate of *Engraulis mordax* in southern California. California Fish and Game 67:62–65.

Goldfeld, S. M., and R. E. Quandt. 1972. Nonlinear methods in econometrics. North-Holland, London.

Lo, N. C. H. 1985. Egg production of the central stock of northern anchovy, *Engraulis mordax*, 1951–82. U.S. National Marine Fisheries Service Fishery Bulletin 83:137–150.

MacCall, A. D. 1974. The mortality rate of *Engraulis mordax* in southern California. California Cooperative Oceanic Fisheries Investigations Reports 17:131–135.

MacCall, A. D., R. A. Klingbeil, and R. D. Methot. 1985. Recent increased abundance and potential productivity of Pacific mackerel (*Scomber japonicus*). California Cooperative Oceanic Fisheries Investigations Reports 26:119–129.

Mais, K. F. 1974. Pelagic fish surveys in the California Current. California Department of Fish and Game Fish Bulletin 162.

Mais, K. F. 1981. Age-composition changes in the anchovy, *Engraulis mordax*, central population. California Cooperative Oceanic Fisheries Investigations Reports 22:82–87.

Methot, R. D. 1986. Synthetic estimates of historical abundance and mortality for northern anchovy, *Engraulis mordax*. U.S. National Marine Fisheries Service, Southwest Fisheries Center, Administrative Report LJ 86-29, La Jolla, California.

Murphy, G. I. 1965. A solution of the catch equation. Journal of the Fisheries Research Board of Canada 22:191–202.

Parker, K. 1980. A direct method for estimating northern anchovy, *Engraulis mordax*, spawning biomass. U.S. National Marine Fisheries Service Fishery Bulletin 78:541–544.

Parrish, R. H., D. L. Mallicoate, and R. A. Klingbeil. 1986. Age dependent fecundity, number of spawnings per year, sex ratio, and maturation stages in northern anchovy, *Engraulis mordax*. U.S. National Marine Fisheries Service Fishery Bulletin 84:503–517.

Parrish, R. H., D. L. Mallicoate, and K. F. Mais. 1985. Regional variations in the growth and age composition of northern anchovy, *Engraulis mordax*. U.S. National Marine Fisheries Service Fishery Bulletin 83:483–496.

Peterman, R. M., M. J. Bradford, N. C. H. Lo, and R. D. Methot. 1988. Contribution of early life stages to interannual variability in recruitment of northern anchovy (*Engraulis mordax*). Canadian Journal of Fisheries and Aquatic Sciences 45:8–16.

PFMC (Pacific Fishery Management Council). 1983. Northern anchovy fishery management plan. PFMC, Portland, Oregon.

Sunada, J. S., and S. Silva. 1980. The fishery for northern anchovy, *Engraulis mordax*, off California and Baja California in 1976 and 1977. California Cooperative Oceanic Fisheries Investigations Reports 21:132–138.

Thomson, C., A. Grover, and W. L. Craig. 1985. Status of the California coastal pelagic fisheries. U.S. National Marine Fisheries Service, Southwest Region, Administrative Report SWR-85-1, Terminal Island, California.

8945

BULLETIN OF MARINE SCIENCE, 44(2): 616–630, 1989

COMMUNITY STRUCTURE, BIOMASS AND PRODUCTIVITY OF DEEPWATER ARTIFICIAL REEFS IN HAWAII

Robert B. Moffitt, Frank A. Parrish and Jeffrey J. Polovina

ABSTRACT

Artificial reef modules constructed of plastic or concrete were deployed at three sites in deep water on Penguin Bank, Hawaii, in October 1985. Fish communities were censused shortly after deployment and irregularly thereafter, by using the manned submersibles Makalii and Pisces V. In determining the aggregated biomass of transient fish species, depth of reef placement was more important than the reef's structural material and configuration. Conversely, reef structural material and configuration were more important than depth in determining the species diversity, richness and perhaps biomass of resident species attracted to these deepwater artificial reefs. Results suggest that small-scale, deepwater artificial reefs in Pacific island areas function primarily as devices for aggregating fish rather than increasing fish production and that reef configuration and structural material are not very important in aggregating transient species.

Many Pacific islands are characterized by their nearshore coral reefs and narrow shelves with steeply sloping sides. The flat, sandy shelves are generally devoid of fish while the deep slopes are home to many commercially important eteline snappers and epinepheline groupers at depths of 100 to 400 m. Penguin Bank, Hawaii, is a large, flat shelf that extends about 50 km southwest of the island of Molokai (Fig. 1). Considerable commercial fishing for deepwater snappers (e.g., *Pristipomoides* spp. and *Etelis* spp.) is conducted on its slopes. Ralston (1984) suggests that this resource may be overfished. Sale (1978) suggests that habitat is a limiting factor in reef fish recruitment. If recruitment of deepwater snappers is similarly limited by habitat, artificial reefs placed on the shelf areas could provide additional habitat for juveniles and presumably increase recruitment of adults to the fishery.

Many of the more recent studies on artificial reef performance have analyzed the effectiveness of specially designed reefs (Sheehy, 1982; Woodhead et al., 1982; Alevizon et al., 1985) as opposed to reefs made by the traditional method of dumping scrap materials (e.g., old car bodies and tires) (Stone et al. 1974; Crowe and McEachron, 1986). Comparing a commercially available artificial reef made of fiberglass-reinforced plastic (FRP) to a traditional reef made of discarded concrete pipe, Sheehy (1983) found considerably higher fish densities at the FRP reef than at the concrete reef.

In our study, FRP and concrete artificial reefs constructed similarly to those in Sheehy (1983) were deployed in deep water (61, 98 and 117 m) on Penguin Bank (Fig. 1). Artificial reefs deployed in shallower water generally have been monitored by divers equipped with scuba gear (Stephens and Zerba, 1981; Hueckel and Stayton, 1982; Kock, 1982); however, the depths in our study made scuba gear impractical, and a manned submersible was used instead. Conducting a visual census of fish communities by using a submersible, though more difficult than using scuba in many respects, has been shown to be practical (Ralston et al., 1986; Thresher and Colin, 1986). Censuses were conducted to determine whether either of the reef types would be used by juveniles of commercially important species (particularly eteline snappers) and to determine whether the results in Sheehy's (1983) study in shallow Atlantic waters could be reproduced in deep Pacific waters.

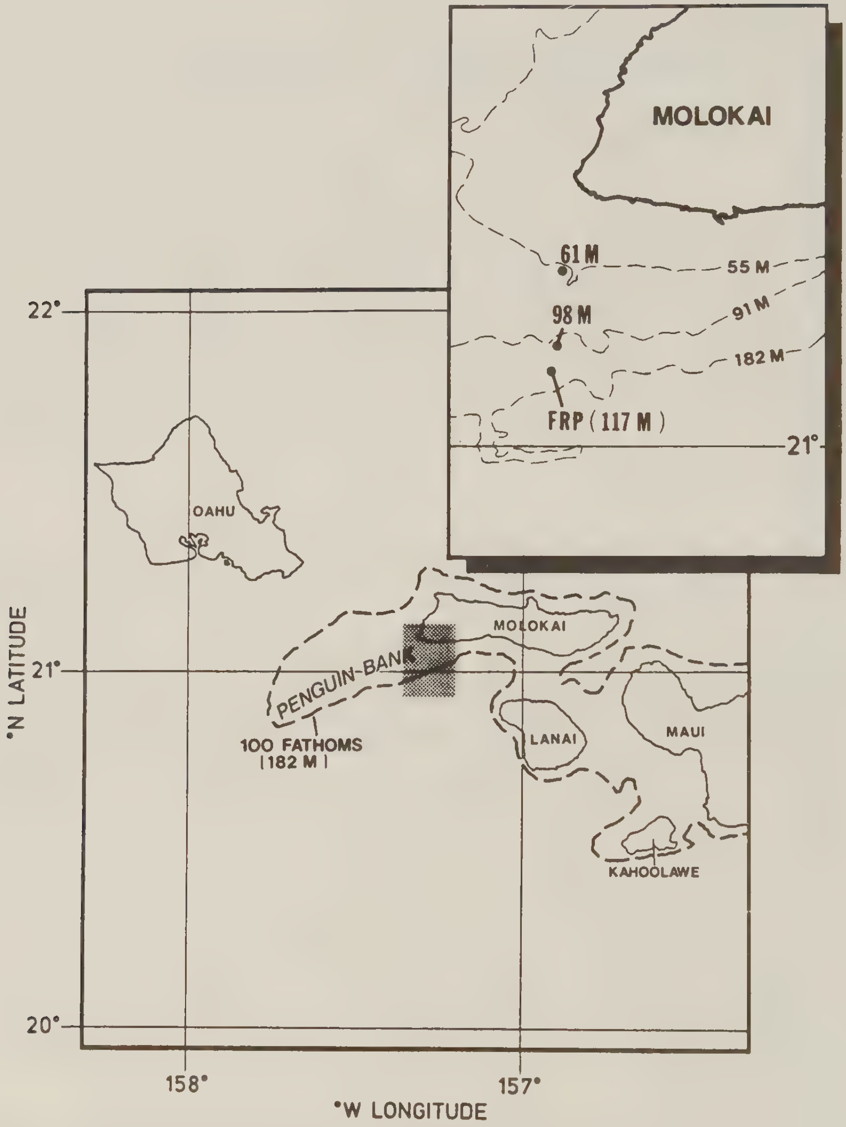


Figure 1. Chart of Penguin Bank with insert indicating artificial reef sites.

If so, then perhaps the greater expense of these specially fabricated reefs could be justified for future artificial reef projects.

Methods

Study Site.—A preliminary dive was conducted on Penguin Bank at depths of 60–150 m by using the submersible Makalii (see Harrison (1986) for a brief description of the submersible). The flat shelf area observed on this dive was very uniform, largely featureless and devoid of fish life. The bottom was mostly sand with a few scattered, low-profile limestone outcroppings and a few small, black coral

Table 1. Specifications and dates of observations of Penguin Bank artificial reefs

Reef site	Depth (m)	Reef height (m)	Enclosed volume (m^3)	Reef surface area (m^2)	Date observed
61 m concrete (four modules)	61	0.8–1.1	5.0	84.0	20 Dec 1985 3 May 1986 13 Oct 1986 10 Apr 1987
98 m concrete (four modules)	98	0.8–1.1	5.6	88.7	18 Oct 1985 19 Dec 1985 6 Feb 1986 2 May 1986 11 Oct 1986 8 Apr 1987 12 Feb 1988
Fiberglass-reinforced plastic (one module)	117	5.3	139	221	16 Oct 1985 19 Dec 1985 6 Feb 1986 2 May 1986 11 Oct 1986 8 Apr 1987 12 Feb 1988

trees. In the deeper areas, less duning of sand was observed, indicating that it may be only a thin layer covering a harder substrate. Periodic currents in the area were strong, up to about 2 knots.

Reef Construction.—The artificial reef modules were constructed of two different types of materials. The first was a commercial FRP module composed of nine cylinders stacked in a pyramid as illustrated in Mottet (1985). The remaining reef modules were constructed of concrete pipe, either 30 cm or 45 cm inside diameter, stacked in low profile pyramids of either three or six pipes. The pipes were bound together with 12.5-mm stainless steel bands and 12.5-mm polypropylene line. Each pipe was fitted with a center barrier equipped with small holes allowing water to flow through, making a cavelike rather than a tunnellike enclosure. The center barriers of the 45-cm-diameter pipes were constructed of poured concrete, whereas the barriers of the 30-cm-diameter pipes were acrylic plastic.

Reef Deployment.—The reef modules were dropped off a large fuel barge at three Penguin Bank sites on 15 October 1985. An acoustic pinger with a 3-year battery pack was attached to one reef module at each site. The FRP reef was dropped in 117 m of water. A group of four concrete modules (two modules were of three 45-cm-diameter pipes and two were of six 30-cm-diameter pipes) was dropped in 98 m of water about 0.8 km north of the FRP reef. The other group of four concrete modules (one module was of three 45-cm-diameter pipes, two were of six 30-cm-diameter pipes and one was of three 30-cm-diameter pipes) was dropped in 61 m of water about 3.2 km north of the FRP reef. The resulting specifications of each reef are listed along with the observation dates in Table 1.

Data Collection and Analysis.—Visual censuses were conducted using the two-man submersible MAKALII, mentioned above, or the larger, three-man submersible PISCES V, which has observational and photographic capabilities similar to the MAKALII (the PISCES V was used for the February 1988 observation only). The fish species observed were categorized as either resident, transient or incidental species (Table 2). Those referred to as resident species are generally small-sized species that use the reef for shelter, probably forage on the reef module or in the immediate vicinity and are likely to be found at the same reef module over a long period. Transient species are generally medium- to large-sized species that aggregate in the vicinity of the reef but do not appear to use it as a refuge and that probably maintain and frequently patrol a large foraging area. Incidental species are defined as those that, although occasionally observed in the vicinity of the reef, show no apparent association with the reef and are just as likely to be seen in the open sand areas with no reef present. Incidental species are excluded from our analyses.

The reef sites were to be monitored quarterly; however, poor weather and problems with submersible maintenance caused several scheduling changes, complicated by the needs of other users. Thus, submersible dives were conducted irregularly. Also, on many occasions, insufficient bottom time, due to strong bottom currents or equipment failure, prevented us from visiting all three reef sites. In these cases, the 61 m reef site was missed.

A visual census was conducted during each site visit (Table 1). The submersible slowly circled each module of each reef visited as an observer counted all fish within sight of the reef and directed video and still camera photography. Fish were identified to the lowest level possible (generally species); the number and estimated size (total length) of individuals of each species were recorded. Slides and videotapes were reviewed later by two observers, who recorded fish counts by species. For transient species, which would swim in and out of view, the estimated total number of individuals of each species was considered to be the largest number seen at any one time during the entire reef visit, as recorded on the field observer logs or the video or slide review logs. For resident species, the estimated total number of individuals of each species was obtained by summing the largest number seen at any one time for each module in a reef. As is the case in any visual census, cryptic species and those that avoid the observer may be underrepresented in these estimates. However, with the relatively open structure of our reefs affording good visual access and the lack of any obvious avoidance of the submersible by those species observed (as similarly reported by Thresher and Colin (1986)), we believe that our counts are reasonably accurate. However, should any bias exist in our sampling of community structure, it should be the same for all study sites, so the comparisons between our reef sites are valid.

Census data were used to calculate four measures of community structure: richness, total number of fish, diversity and standing stock biomass. Richness (number of species) and total number of individuals present within a population are rough indicators of community structure. More sophisticated is the diversity index, which in this case is Brillouin's function for a fully censused population (Pielou, 1977) and includes factors related to the number of species present (richness) and the number of individuals found within each species (evenness). Standing stock biomass was estimated by substituting our fish length estimates in published (Yamaguchi, 1953; Uchiyama et al., 1984) and unpublished length-weight functions (James Parrish, University of Hawaii, Cooperative Fisheries Unit, Honolulu, Hawaii 96822, 1987, pers. commun.). Transient and resident species assemblages were treated separately for all measures. Paired t-tests were used to determine whether any differences between the four measures by reef sites were significant at the 0.05 level.

RESULTS

No problems were encountered in deployment of the reef modules. Modules of the two concrete reefs landed in a linear arrangement, with roughly 15–30 m between adjacent modules. This was generally within visual range, depending on visibility. Some of the acrylic partitions in the 30-cm-diameter pipe modules broke during deployment; otherwise, the reef modules landed well and were undamaged. Although some scouring was observed at all sites, the reef modules remained relatively stable throughout the study. Large pits and the threat of module burial occurred only at the 61 m reef site, where the sand layer appears to be deeper.

Our reefs are almost certainly unfished. The location of the reefs has not been disclosed to date, and because of the small size of our reefs and their distance from traditional fishing areas, we believe it unlikely that any fishermen have been able to find them. No signs of fishing activity were noted during our observations. Therefore, all of the results discussed below are viewed as products of unfished artificial reefs.

Transient species were the first to arrive at our reef sites. Several of the larger transient species (e.g., *Seriola dumerili*, *Naso* spp. and *Pristipomoides filamentosus*) recruited to the reef sites within 24 to 72 h after deployment. Values for richness of transient species were very similar for all reef sites, beginning at moderate levels and showing a general increase over time (Fig. 2A). Most of the transient species that appeared later were the smaller species (e.g., *Acanthurus* spp., *Synodus* spp. and *Coris* spp.). Results of paired t-tests showed no significant differences in richness of transient species between any of the three possible reef comparisons. Calculation of recruitment curves using the formula $y = a(1 - e^{-b(t+c)})$ gives asymptotic values for transient species richness of 8.9 (asymptotic standard deviation (SD) = 4.2, $R^2 = 0.57$), 11.4 (SD = 3.6, $R^2 = 0.27$) and 35.2

Table 2. List of species of transient, resident and incidental fishes observed by reef type (T = transient species, R = resident species, I = incidental species, 61 m and 98 m = concrete reefs, FRP = fiberglass-reinforced plastic reef)

Taxonomic classification	Species group	Reef type
Acanthuridae		
Acanthurus dussumieri	T	61 m, 98 m, FRP
Acanthurus xanthopterus	T	61 m, 98 m, FRP
Naso brevirostris	T	61 m
Naso spp.*	T	61 m, 98 m, FRP
Naso unicornis	T	61 m
Zanclus cornutus	R	61 m
Apogonidae		
Apogon spp.†	R	61 m, 98 m, FRP
Aulostomidae		
Aulostomus chinensis	T	61 m, 98 m, FRP
Balistidae		
Cantherines verecundus	T	61 m, 98 m
Osbeckia scripta	T	FRP
Prevagor spilosoma	T	61 m, 98 m, FRP
Sufflamen fraenatus	T	61 m, 98 m
Bothidae	I	61 m
Carangidae		
Caranx ignobilis	T	98 m
Caranx melampygus	T	98 m
Carangoides orthogrammus	T	98 m, FRP
Decapterus macarellus	I	61 m
Seriola dumerili	T	61 m, 98 m, FRP
Chaetodontidae		
Chaetodon fremblii	R	61 m, 98 m
Chaetodon kleinii	R	61 m
Chaetodon miliaris	R	61 m, 98 m
Forcipiger sp.‡	R	98 m
Heniochus acuminatus	R	61 m, 98 m
Congridae		
Conger sp.	R	FRP
Diodontidae		
Diodon hystrix	I	98 m
Gobiidae	R	FRP
Holocentridae		
Holocentrinae	R	61 m, 98 m
Myripristinae		
Myripristis chryseres	R	FRP
Labridae		
Anampses chrysocephalus	R	61 m, 98 m
Bodianus bilunulatus	T	98 m
Coris ballieui	T	98 m
Coris flavovittata	T	98 m
Coris gaimardi	R	61 m
Hemipteronotus pavoninus	I	61 m
Labroides phthirophagus	R	61 m, 98 m
Lutjanidae		
Aprion virescens	T	98 m, FRP
Lutjanus kasmira	R	61 m, FRP
Pristipomoides filamentosus§	T	98 m, FRP
Mugiloididae		
Parapercis roseoviridis	I	98 m
Mullidae		
Mulloidichthys sp.‖	T	61 m, 98 m, FRP
Parupeneus multifasciatus	T	61 m, 98 m
Parupeneus pleurostigma	T	61 m, 98 m
Parupeneus porphyreus	T	98 m, FRP

Table 2. Continued

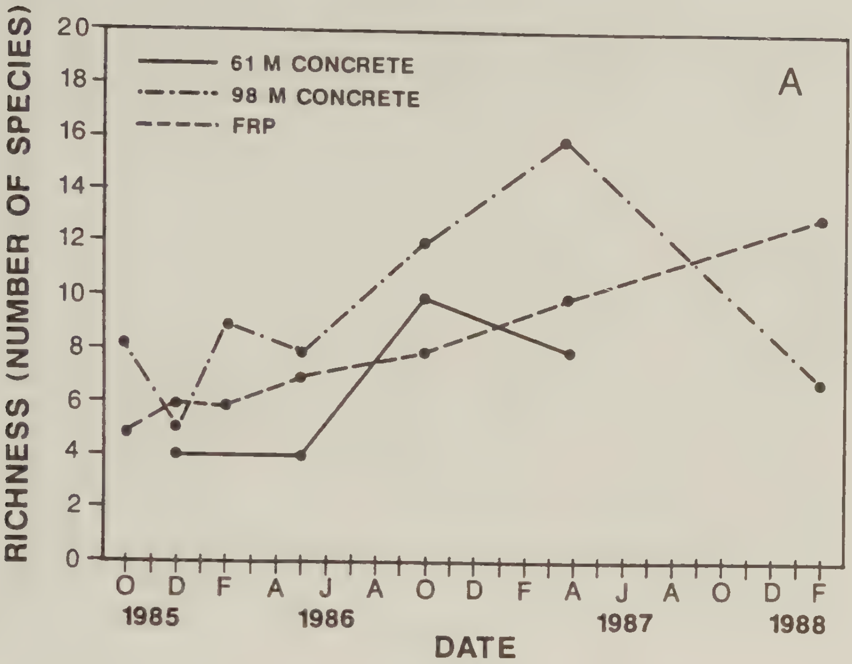
Taxonomic classification	Species group	Reef type
Muraenidae		
Gymnothorax flavimarginatus	R	98 m
Gymnothorax steindachneri	R	61 m
Ophidiidae		
Brotula multibarbata	T	98 m
Pentacerotidae		
Evistias typus	R	FRP
Pomacanthidae		
Holacanthus arcuatus	R	61 m, 98 m
Centropyge potteri	R	98 m
Pomacentridae		
Dascyllus albisella	R	61 m
Chromis ovalis	R	61 m, 98 m
Chromis verater	R	61 m, 98 m, FRP
Priacanthidae		
Priacanthus sp.#	R	61 m, 98 m
Scorpaenidae		
Dendrochirus barberi	R	61 m, 98 m
Pterois sphex	R	98 m
Scorpaena ballieui	R	98 m, FRP
Serranidae		
Anthias thompsoni	R	61 m, 98 m, FRP
Anthias ventralis	R	98 m, FRP
Holanthias fuscipinnis	R	98 m, FRP
Synodontidae	T	61 m, 98 m, FRP
Tetraodontidae		
Canthigaster coronatus	R	61 m, 98 m
Canthigaster epilampra	R	98 m, FRP

* Includes *N. maculatus* and *N. hexacanthus*.
† Includes *A. maculiferus* and *A. kallopterus* and perhaps others as well.
‡ May be *F. longirostris* or *F. flavissimus*.
§ May include *Pristipomoides sieboldii* and *Aphareus rutilans* as well.
‖ May be *M. vanicolensis* or *M. pflugeri*.
# Probably *P. alalaua*, which may be a synonym of *P. hamrur*.

species (SD = 267.5, $R^2 = 0.98$) for the 61 m concrete, 98 m concrete and FRP reefs, respectively. Ninety percent of these species are predicted to be present at the reefs within 15, 10 and 213 months, respectively. The unusually large asymptotic richness and lengthy time estimated to 90% recruitment values seen at the FRP reef are not significantly different from those obtained from the other two reef sites and are due to the apparent linear growth in richness, which forces the recruitment model to estimate an unrealistically large asymptotic level. Presumably, a longer time series at the FRP reef would show richness leveling off in the 9–15 species range, similar to that of the other two reef sites.

The number of individual fish of transient species varied considerably at each site over time (Fig. 3A). Between sites, however, the number of fish was usually similar and tended to fluctuate in a parallel fashion over time. No significant differences between reef pairs were observed in paired *t*-tests. Peaks in May 1986 and April 1987 at all sites indicated a possible seasonal change in abundance of transient fish.

Differences between reefs were apparent in the diversity of transient fish species (Fig. 4A). The 98 m and FRP reefs showed remarkably similar changes in diversity over time: Diversity was moderate initially, increased slightly in the first 4 months, then remained relatively stable for the duration of the study. The 61 m reef, however, had relatively low initial diversity, with a one-time peak into the mod-



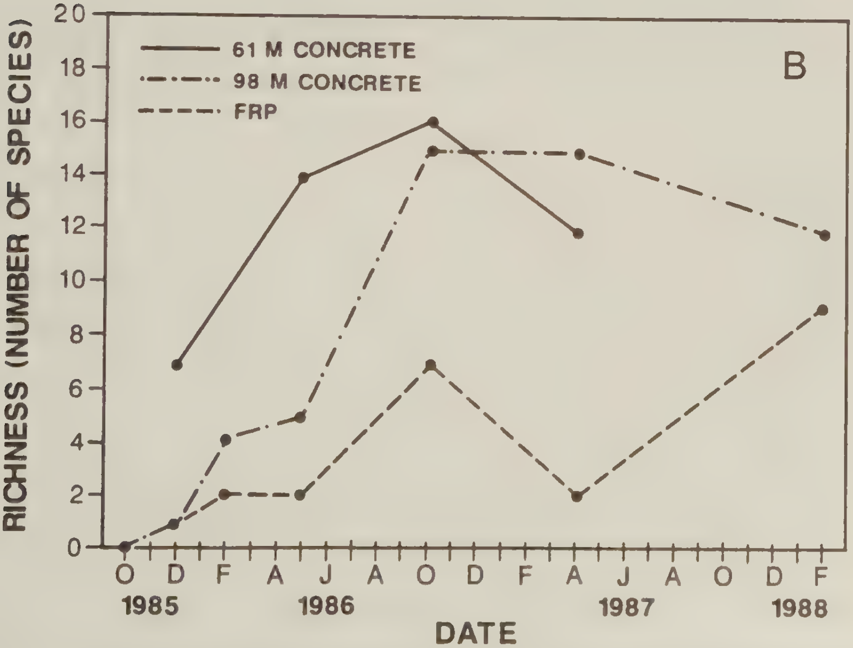


Figure 2. Richness at Penguin Bank artificial reefs. (A) Transient species. (B) Resident species.

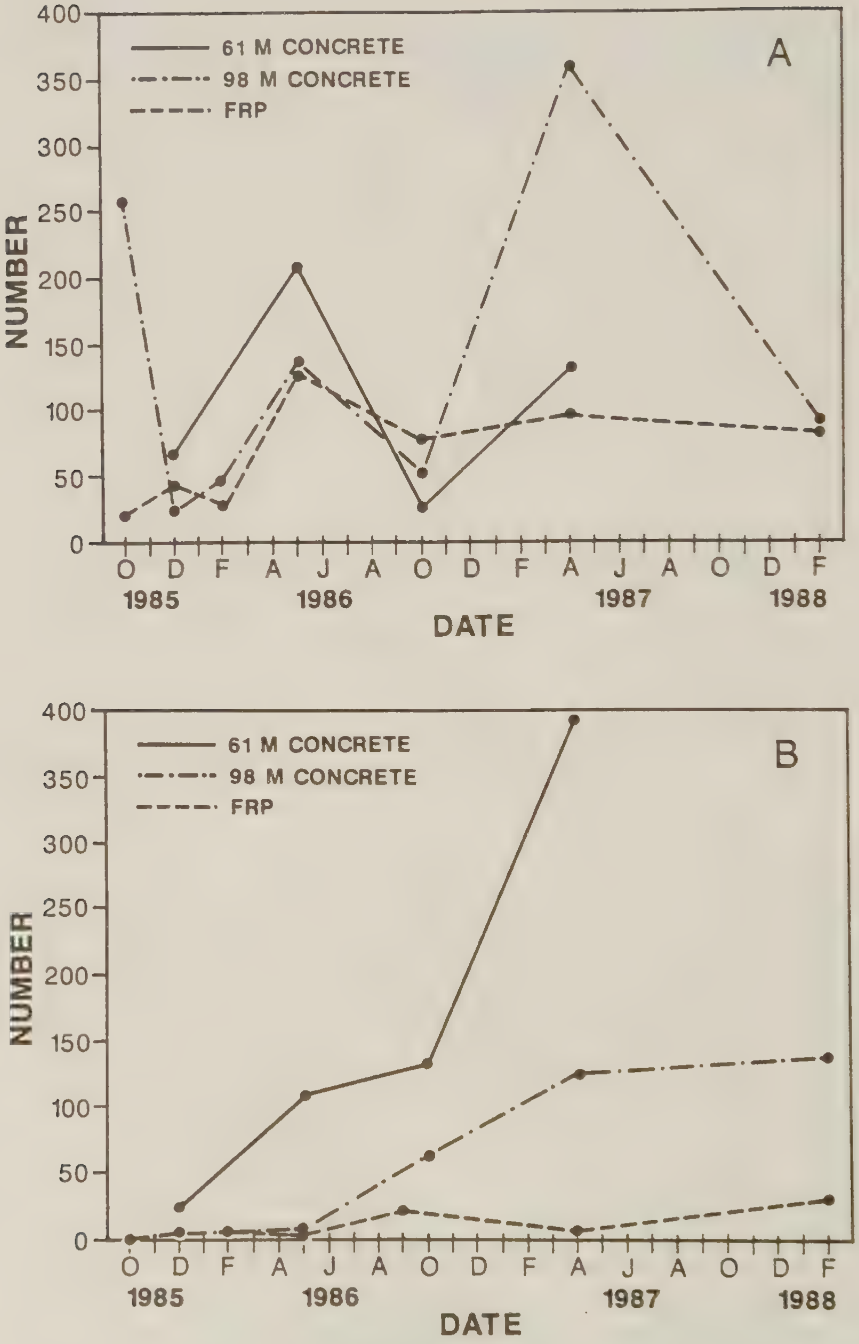


Figure 3. Number of fish at Penguin Bank artificial reefs. (A) Transient species. (B) Resident species.

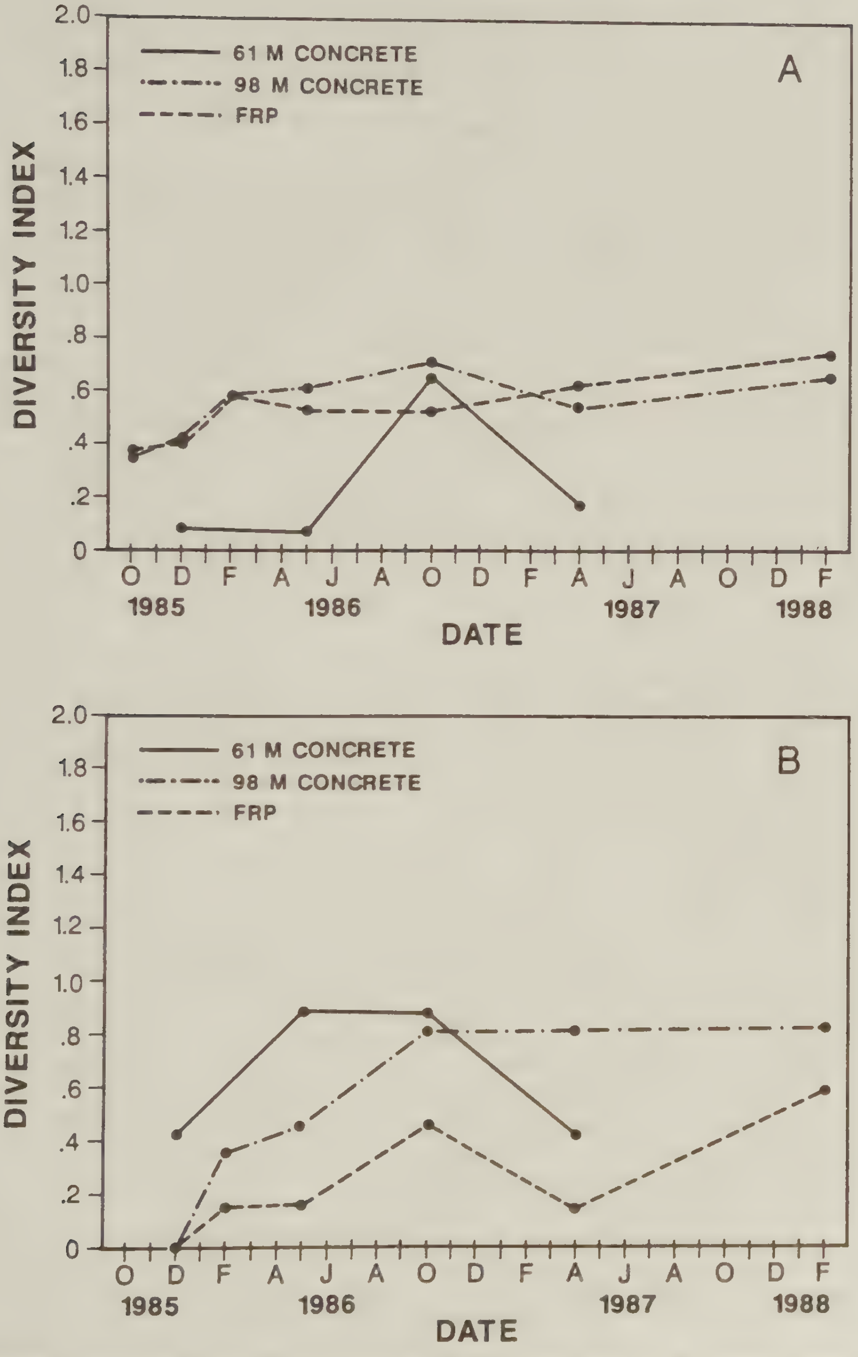


Figure 4. Diversity at Penguin Bank artificial reefs. (A) Transient species. (B) Resident species.

erate range in October 1986, followed by a return to a low level. Paired *t*-test analysis indicated a significant difference in the diversity of transient species between the 61 m and 98 m concrete reefs, but no significance in other paired comparisons. Because the richness and numbers of individuals of transient species were similar at these sites, the significantly lower diversity value of the 61 m reef must be largely due to a lack of evenness.

Despite the similarity in the total numbers of transient fish between reef sites throughout the study, standing stock biomass estimates for the 61 m concrete reef were much lower than those of the other two reefs (Fig. 5A). Paired comparisons indicated a significant difference between the 61 m concrete reef and the FRP reef, but no significance in the other paired comparisons. Over 90% of the biomass of transient species at the 98 m and FRP reefs was attributable to four species designations, *Aprion virescens, Naso* spp., *Pristipomoides filamentosus* and *Seriola dumerili*. These four were the largest of the transient species observed in our study and, by contrast, comprised less than 1% of the biomass at the 61 m site. These differences in the relative contribution to the biomass of transient species may be due to differences in depth, distance from the bank dropoff or random site factors not identified because of the lack of replicates at any single depth. In the same manner, the great similarities in biomass and species contributions of transient species at the 98 m and FRP reefs, despite large differences in reef size (e.g., height, volume and surface area) and structural material, suggest that depth (or location on the bank) is more important than reef size or structural material in determining attracted biomass.

Temporal patterns in community structure measures for resident species were very different from those for transient species. The richness of resident species (Fig. 2B) started at 0 at the 98 m and FRP reefs, as would be expected (the 61 m reef was not visited until 2 months after deployment). Resident species richness at the 61 m and 98 m concrete reefs increased rapidly, then leveled off at about 12 months. The FRP reef showed a much slower increase in richness, with no apparent leveling out by the end of the study. Paired *t*-test analysis indicated a significant difference in richness between the 61 m concrete and FRP reefs, but no significant difference between other pairs. Recruitment curves generated for resident species richness indicated asymptotic values of 14.0 (SD = 0.0029, R^2 = 0.82), 15.1 (SD = 3.6, R^2 = 0.85) and 58.8 species (SD = 345.6, R^2 = 0.60) for the 61 m, 98 m and FRP reefs, respectively. Ninety percent of these species are predicted to be present within 2.8, 20 and 461 months, respectively. As with the transient species, no significant differences in asymptotic richness values for resident species were apparent between the reef sites. Again, a longer time series of observations at the FRP reef presumably would show a leveling off of resident species richness yielding an asymptotic value of about 14–15 species, as seen at the other two reef sites. The significant difference in richness between the 61 m and FRP reefs is probably due to differences in the rate of colonization rather than to the number of species in the available pool.

No significant difference was found in the number of individuals of resident fish at the three reef sites throughout the study. However, trends in the number of individuals over time (Fig. 3B) suggest that the two concrete reefs recruit earlier and hold more resident fish than the FRP reef. The unusually large number of fish observed at the 61 m concrete reef in April 1987 was mostly due to a very large aggregation of *Priacanthus* sp. encountered at a single reef module. We believe this was a temporary phenomenon, possibly a breeding aggregation. Unfortunately, submersible dives scheduled for fall 1987 were cancelled and attempts to locate the 61 m reef in February 1988 were unsuccessful.

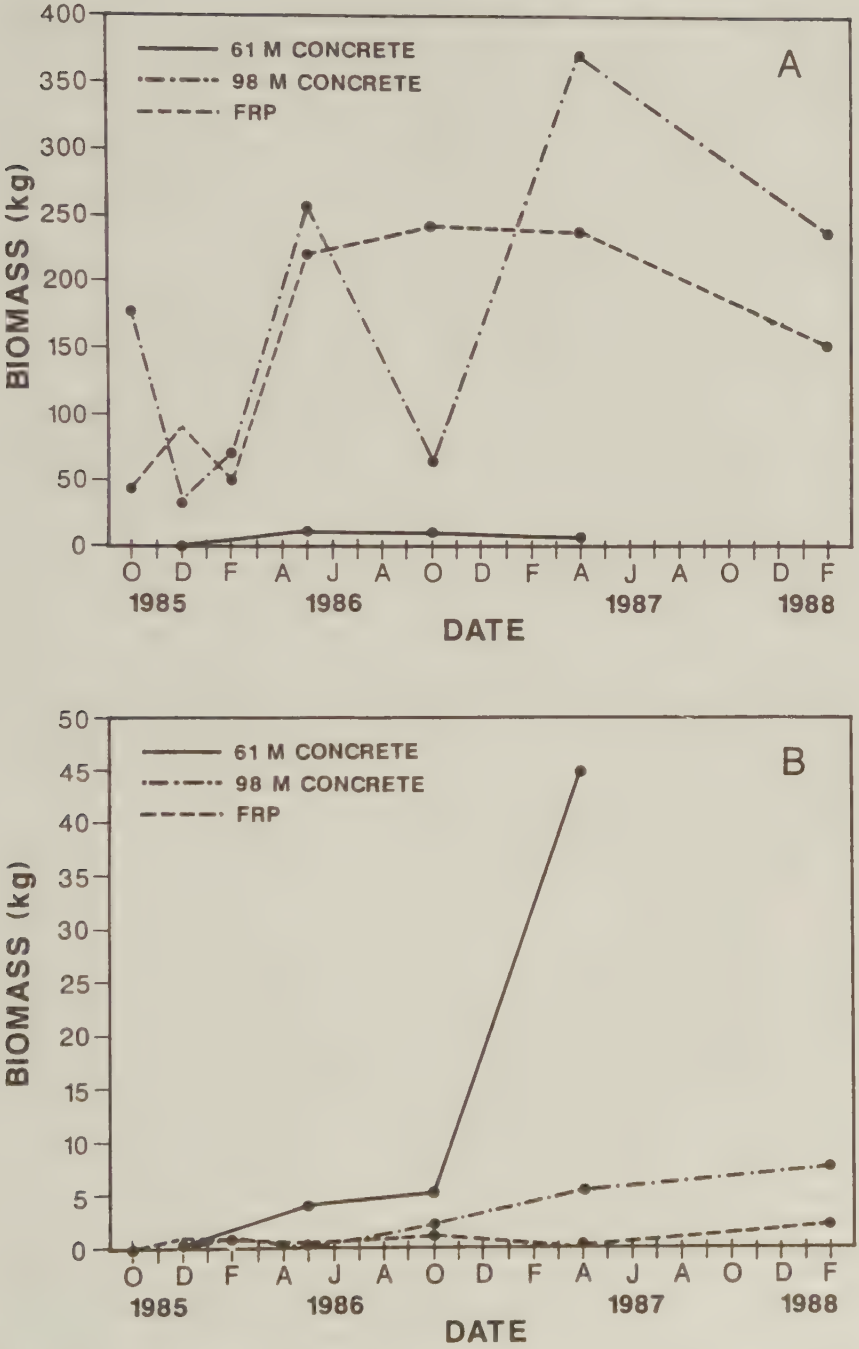


Figure 5. Biomass at Penguin Bank artificial reefs. (A) Transient species. (B) Resident species.

As with richness and number, the diversity of resident fish at the FRP reef was lower than at the concrete reefs (Fig. 4B). These differences were significant, whereas those between the 61 m and 98 m concrete reefs were not.

The pattern of biomass of resident species over time for the three reefs (Fig. 5B) was, again, similar to those of richness, number and diversity. The 61 m concrete reef had the earliest increase and highest biomass values, followed by the 98 m concrete reef. The FRP reef had the slowest rise and lowest values throughout the study. Results of paired *t*-tests indicated no significant differences between any pairs.

In the above results, all reefs were treated as single units. The two concrete reefs, however, were each composed of four individual modules. Transient fish species swam freely between modules during an observation period and, therefore, could not be attributed to a single module. Resident fish, on the other hand, were restricted to a single module during an observation period and were recorded as such. These modules, then, can be considered as replicates for each site and depth. Because the means and variances of each of the measures are expected to change over time, comparisons must be made on an observation date by observation date basis. The variance between treatments was about double that within a treatment; hence, no significant differences between resident species at the 61 m and 98 m concrete reefs were shown for any of the four measures.

Most individuals of both transient and resident species recruited to our reefs as adults. Of the few species at least partially recruited to our reefs as small juveniles, most were resident species. Small juveniles observed included the resident species *Dascyllus albisella, Anthias thompsoni, A. ventralis, Chaetodon fremblii, C. miliaris, Chromis verater, Labroides phthirophagus* and *Lutjanus kasmira* and the transient species *Synodus* sp. and *Coris flavovittata.* Even among these species, most of the recruitment appeared to occur from adult immigration. No juvenile eteline snappers were seen at any reef site. Although we had hoped to attract some, it is not entirely surprising that they were not seen. To date, the nursery habitat for these species has not been located so their absence from our reefs may be due to incorrect placement of our reefs and not necessarily to reef design.

Discussion

Our study compares most directly with that of Sheehy (1983), who evaluated both concrete conduit and FRP reefs. The major differences are that (1) his study was conducted in about 30 m of water on the continental shelf in the Atlantic Ocean, (2) the concrete conduit in his study was dumped as single pieces rather than being fabricated into reef modules and (3) his reef sites were heavily fished by anglers. Sheehy (1983) showed that the FRP reefs aggregated about 10 times as many fish as the concrete conduit reefs. On the other hand, our results show a great similarity between the 98 m concrete reef and the FRP reef in their ability to aggregate transient species, despite vast differences in size, structural material and design. Furthermore, the 61 m reef was a relatively poor aggregator of transient species, despite similarities to the 98 m reef in size, structural material and design. These results suggest that depth and location on the bank are more important than size, structural material and design in attracting transient species biomass. In contrast, the two concrete reefs outperformed the FRP reef in all measures analyzed for resident species and showed a greater similarity to each other than to the FRP reef, suggesting that structural material and design are more important than reef depth and location in attracting resident species. From a commercial perspective, the transient species attracted to our reefs are of much greater im-

Table 3. Biomass as a function of reef size (average of October 1986 and April 1987 observations)

Reef site	Mean biomass (kg)	Biomass in terms of size			
		Volume (kg m^{-3})	Surface area (kg·m^{-2})	Cover area (kg m^{-2})	Height (kg·m^{-1})
61 m concrete					
Transient species	7.68	1.54	0.09	0.97	6.98
Resident species	24.67	4.93	0.29	3.11	22.42
98 m concrete					
Transient species	218.09	38.94	2.46	25.84	198.26
Resident species	3.77	0.67	0.04	0.45	3.43
Fiberglass-reinforced plastic					
Transient species	239.74	1.72	1.08	5.61	45.23
Resident species	0.70	0.005	0.003	0.02	0.13

portance than the resident species, both in terms of price per kilogram and the actual biomass attracted.

The size of an artificial reef has been reported to be very important to its ability to attract transient species. Ogawa et al. (1977) found that production increased directly with reef volume up to a critical point of 4,000 m^3. Molles (1978) reported the importance of reef height in attraction of transient species, as did Mottet (1985) who further suggested that the importance of reef height increases with increasing depth. Reef height and volume did not appear to be important in attracting transient species in our study, however. Our 98 m and FRP reefs attracted very similar biomass and numbers of transient fish despite vast differences in reef height and volume (Table 3). When biomass is viewed as a function of reef size in terms of volume, area or height, the 98 m concrete reef appears to out perform the FRP reef by factors of anywhere from 3:1 to nearly 40:1. We believe that in our particular study, however, it is not so much a matter of better performance of the 98 m reef compared to the FRP reef as it is the lack of importance of reef size in attracting the transient fish species involved.

In general, one would expect species richness to be inversely correlated to depth, as has been shown to be true for insular species at Enewetak Atoll, Marshall Islands, by Thresher and Colin (1986). Brock (1980), who generated a recruitment curve for fish species colonizing a newly developed harbor near Kona, Hawaii, reported an asymptotic value of 87.52 species for a surface to 5-m-deep study area. Asymptotic values for richness in our study are comparable to other studies using total species richness, simply by adding the two values for transient and resident species. The values for total richness for the 61 m concrete, 98 m concrete and FRP reefs are 22.9, 26.5 and 94.0 species, respectively. As mentioned earlier, the 94.0 species value obtained for the FRP reef is considered to be unrealistic because colonization has not progressed past the straight-line portion of the recruitment curve at this time. The 22.9 and 26.5 species values obtained for the two concrete reefs are considered to be more realistic and are, in deed, less than the 87.52 species predicted by Brock (1980) for his shallower site. For a 4.2-m-deep shipwreck artificial reef in the eastern Mediterranean Sea, Diamant et al. (1986) reported asymptotic richness values for this reef were 22 species based on visual census data and 37 species based on rotenone collection data. The Mediterranean Sea is a species-poor area (Diamant et al., 1986), which gives predicted asymptotic richness values similar to our much deeper sites.

Considering the similarity of the deep slope transient species throughout the central and western Pacific, the results of our study should be useful in determining future applications of deepwater artificial reefs in the Pacific. We stress that artificial reefs should be viewed and used as management tools. Small-scale artificial reefs, such as those used in this study, do indeed work well as aggregators of commercially important deep slope fish and, therefore, could probably be used to increase the catch per unit effort for these species. They probably will not, however, provide additional nursery habitat for these species or add much to the overall standing stock through new or improved adult habitat. Therefore, their use should be restricted to target species that are currently underutilized. If used to aggregate individuals of overfished species in an unregulated fishery, such as the deep snappers at Penguin Bank, these artificial reefs could add to the problem rather than provide a solution.

Literature Cited

Alevizon, W. S., J. C. Gorham, R. Richardson and S. A. McCarthy. 1985. Use of man-made reefs to concentrate snapper (Lutjanidae) and grunts (Haemulidae) in Bahamian waters. Bull. Mar. Sci. 37: 3–10.

Brock, R. E. 1980. Colonization of marine fishes in a newly created harbor, Honokohau, Hawaii. Pacific Sci. 34: 313–326.

Crowe, A. and L. W. McEachron. 1986. A summary of artificial reef construction on the Texas coast. Texas Parks and Wildlife Department. Management Data Series 98: 1–67.

Diamant, A., A. Ben Tuvia, A. Baranes and D. Golani. 1986. An analysis of rocky coastal eastern Mediterranean fish assemblages and a comparison with an adjacent small artificial reef. J. Exp. Mar. Biol. Ecol. 97: 269–285.

Harrison, J. T., III. 1986. Recent marine studies at Enewetak Atoll, Marshall Islands. Bull. Mar. Sci. 38: 1–3.

Hueckel, G. J. and R. L. Stayton. 1982. Fish foraging on an artificial reef in Puget Sound, Washington. U.S. Natl. Mar. Fish. Serv., Mar. Fish. Rev. 44(6–7): 38–44.

Kock, R. L. 1982. Patterns of abundance variation in reef fishes near an artificial reef at Guam. Env. Biol. Fish. 7: 121–136.

Molles, M. C., Jr. 1978. Fish species diversity on model and natural reef patches: experimental insular biogeography. Ecol. Monogr. 48: 289–305.

Mottet, M. G. 1985. Enhancement of the marine environment for fisheries and aquaculture in Japan. Pages 13–112 *in* F. M. D'Itri, ed. Artificial reefs. Lewis Publishers, Inc., Chelsea, Michigan.

Ogawa, Y., S. Takeuchi and A. Hattori. 1977. An estimate for the optimum size of artificial reef. Bull. Jap. Soc. Fish. Oceanogr. 30: 39–45.

Pielou, E. C. 1977. Mathematical ecology. John Wiley and Sons, New York. 385 pp.

Ralston, S. 1984. Biological constraints on production and related management issues in the Hawaiian deepsea handline fishery. Pages 248–264 *in* R. W. Grigg and K. Y. Tanoue, eds. Proceedings of the second symposium on resource investigations in the Northwestern Hawaiian Islands, Vol. 1. Sea Grant Miscellaneous Report UNIHI-SEAGRANT-MR-84-01.

———, R. M. Gooding and G. M. Ludwig. 1986. An ecological survey and comparison of bottom fish resource assessments (submersible versus handline fishing) at Johnston Atoll. Fish. Bull. U.S. 84: 141–155.

Sale, P. F. 1978. Coexistence of coral reef fishes—a lottery for living space. Env. Biol. Fish. 3: 85–102.

Sheehy, D. J. 1982. The use of designed and prefabricated artificial reefs in the United States. U.S. Natl. Mar. Fish. Serv., Mar. Fish. Rev. 44(6–7): 4–15.

———. 1983. Evaluation of Japanese designed and American scrap material artificial reefs. Aquabio, Inc. Research and Development Report No. 83-RD-607. 73 pp.

Stephens, J. S. and K. E. Zerba. 1981. Factors affecting fish diversity on a temperate reef. Env. Biol. Fish. 6: 111–121.

Stone, R. B., C. C. Buchanan and F. W. Steimle, Jr. 1974. Scrap tires as artificial reefs. Summary Report SW-119. U.S. Environmental Protection Agency. 33 pp.

Thresher, R. E. and P. L. Colin. 1986. Trophic structure, diversity and abundance of fishes of the deep reef (30–300 m) at Enewetak, Marshall Islands. Bull. Mar. Sci. 38: 253–272.

Uchiyama, J. H., S. H. Kuba and D. T. Tagami. 1984. Length-weight and standard length-fork length relationships of deepsea handline fishes of the Northwestern Hawaiian Islands. Pages 209–225 *in* R. W. Grigg and K. Y. Tanoue, eds. Proceedings of the second symposium on resource investigations in the Northwestern Hawaiian Islands, Vol. 2. Sea Grant Miscellaneous Report UNIHI-SEAGRANT-MR-84-01. 353 pp.

Woodhead, P. M. J., J. H. Parker and I. W. Duedall. 1982. The coal-waste artificial reef program (C-WARP): a new resource potential for fishing reef construction. U.S. Natl. Fish. Serv., Mar. Fish. Rev. 44(6–7): 16–23.

Yamaguchi, Y. 1953. The fishery and the biology of the Hawaiian opelu, *Decapterus pinnulatus* (Eydoux and Souleyet). Master's Thesis, Univ. Hawaii, Honolulu. 125 pp.

DATE ACCEPTED: April 28, 1988.

ADDRESS: *NOAA National Marine Fisheries Service, Southwest Fisheries Center, Honolulu Laboratory, 2570 Dole Street, Honolulu, Hawaii 96822-2396.*

8946

Deep-Sea Research, Vol. 36, No. 2, pp. 191–209, 1989.
Printed in Great Britain.

0198–0149/89 \$3.00 + 0.00
© 1989 Pergamon Press plc.

Particulate matter and nutrient distributions in the ice-edge zone of the Weddell Sea: relationship to hydrography during late summer

David M. Nelson,* Walker O. Smith Jr,† Robin D. Muench,‡ Louis I. Gordon,*
Cornelius W. Sullivan§ and David M. Husby||

(*Received* 19 *April* 1988; *in revised form* 24 *August* 1988; *accepted* 6 *September* 1988)

Abstract—Previous estimates of the marginal ice zone's quantitative contribution to biogeochemical cycles and annual productivity in the Southern Ocean may be conservative because of assumptions that phytoplankton blooms are associated only with actively retreating ice edges. Observations during March 1986, near an almost stationary ice edge in the northwestern Weddell Sea, revealed very low geostrophic currents, no appreciable horizontal gradients in temperature or salinity and no significant net melting or freezing in the ice-edge region. Vertical stratification within the upper 50 m was evident throughout the study area, and resulted primarily from prior melting of pack ice. In contrast with previous observations in marginal ice zones, the distribution of phytoplankton biomass showed little correlation with the meltwater field; here, significant horizontal biomass gradients occurred in an area where vertical stability was almost uniform laterally and both elevated biomass and diminished nutrient levels extended well below the pycnocline. Absolute levels of chlorophyll were modest (generally <0.7 $\mu g\ l^{-1}$), but the highest particulate carbon, nitrogen and biogenic silica values (>10, 1.5 and 3.5 $\mu mol\ l^{-1}$, respectively) were similar to those found previously during a spring phytoplankton bloom at the Weddell–Scotia Sea ice edge. The mean mole ratio of biogenic silica to organic carbon within the particle assemblage was 0.44, which is very high for surface seawater and about three times higher than that typically found in pure diatom cultures. Therefore, despite relatively low chlorophyll levels, the ice edge remained a localized maximum in biogenic particulate matter at least through March and this material was unusually rich in silica. Combined, these physical and biological data show that elevated phytoplankton biomass in the ice-edge zone can persist well past the time when net melting stops and the ice edge becomes stationary.

INTRODUCTION

In polar and subpolar oceans that experience seasonal advance and retreat of pack ice, phytoplankton blooms in the ice-edge zone are a major component of the annual cycle of biogenic particle production. In all marginal ice zones studied to date, phytoplankton biomass levels have been substantially higher than those observed either under the ice or seaward of the region affected hydrographically by ice melt, e.g. the Bering Sea (Alexander and Niebauer, 1981), the Ross Sea (Smith and Nelson, 1985), Fram Strait (Smith *et al.*, 1987) and the Weddell–Scotia Sea (Nelson *et al.*, 1987). Despite major

---

* College of Oceanography, Oregon State University, Corvallis, OR 97331, U.S.A.

† Botany Department and Graduate Program in Ecology, The University of Tennessee, Knoxville, TN 37996, U.S.A.

‡ Science Applications International Corporation, 13400B Northrup Way, Suite 36, Bellevue, WA 98005, U.S.A.

§ Department of Biological Sciences, University of Southern California, Los Angeles, CA 90089, U.S.A.

|| Southwest Fisheries Center, NMFS, National Oceanic and Atmospheric Administration, P.O. Box 831, Monterey, CA 93942, U.S.A.

differences in hydrographic conditions, nutrient concentrations, surface irradiance and biological features among ice-edge systems in different geographic locations, these past studies have indicated that vertical stability within the upper 100 m is essential for the growth and accumulation of biogenic material and may be the single most important factor regulating these processes. This appears to be particularly true in the Southern Ocean, where major nutrient concentrations are rarely, if ever, low enough to limit phytoplankton growth. Because the density of seawater is controlled almost entirely by salinity at low temperatures, ice melt creates a mesoscale region of vertical stability with high phytoplankton biomass and productivity. This mesoscale bloom has a significant impact on the annual productivity, trophic dynamics and biogeochemical cycles of the entire Southern Ocean (SMITH and NELSON, 1986; AINLEY *et al.*, 1986; NELSON and SMITH, 1986). However, major uncertainties remain as to these blooms' duration and magnitude, especially during the late summer/early autumn period, from which virtually no data have been available.

A previous study in the Weddell–Scotia Sea in spring showed that the ice-edge zone was the site of localized maxima in chlorophyll *a*, and particulate carbon, nitrogen and biogenic silica, and that these increased levels correlated spatially with the density structure (NELSON *et al.*, 1987). Mixed-layer depths in that study ranged from about 20 to 150 m, and Chl *a* concentrations ranged from <0.2 μg l^{-1} under the ice and <0.5 μg l^{-1} at stations with deep mixed layers >300 km from the ice edge to values typically >5 μg l^{-1} within the bloom. The highest Chl *a* levels observed were >30 μg l^{-1} at one station near the ice (W. O. SMITH, unpublished data). Particulate carbon, nitrogen and biogenic silica showed similar distributions. A satellite image of pigment concentration confirmed these distributions, and also substantiated the shipboard observation that there was significant along-ice variation in particulate matter concentrations (NELSON *et al.*, 1987). These observations in the Weddell–Scotia Sea, taken together with a summer study of the ice-edge zone in the Ross Sea (SMITH and NELSON, 1985; WILSON *et al.*, 1986; NELSON and SMITH, 1986), indicate that the growth and accumulation phase of phytoplankton blooms in the marginal ice zone can be initiated early in the spring (no later than late October) and continues at least through early February, following the ice edge as it retreats. However, understanding of the degradation phase of this feature (its timing and its causal mechanisms) has been hampered by a shortage of late summer and autumn data on appropriate spatial scales.

In March 1986 we conducted a study in the marginal ice zone of the western Weddell Sea as part of the AMERIEZ (Antarctic Marine Ecosystem Research at the Ice-Edge Zone) project. Our goal was to determine the magnitude of any ice-edged phytoplankton bloom and to assess its dependence on the mesoscale density structure, circulation patterns and nutrient fields. We also sought to obtain the first data on the degradation phase of an ice-edge bloom in late summer so that estimates of annual productivity of Southern Ocean marginal ice zones (e.g. SMITH and NELSON, 1986; SMITH *et al.*, in press) could be made more accurate. We report here the distributions of temperature, salinity, nutrients and biogenic particulate matter that characterized the Weddell Sea ice-edge zone in March, and compare these distributions with the conditions observed in this and other ice-edge zones during austral spring and summer.

The study area extended westward from the deep basin of the central Weddell Sea onto the continental rise off the eastern coast of the Antarctic Peninsula (Fig. 1). Bottom depths in the eastern portion of this region exceeded 4500 m and shoaled to <3500 m at

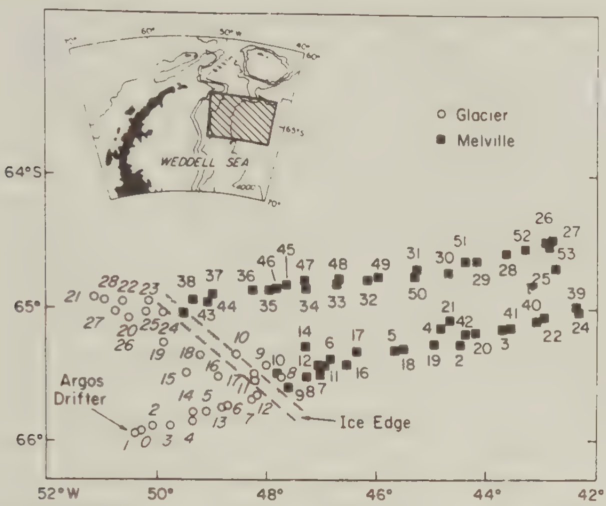


Fig. 1. Study area and station locations. An Argos-tracked buoy was deployed on a large ice floe at the location shown.

the westernmost stations. The region is situated more than 100 km east of the continental slope of the Antarctic Peninsula and more than 200 km south of the shoal region (<3000 m) and extends eastward from the tip of the Antarctic Peninsula. It lies more than 200 km south of the considerably shallower banks surrounding the South Orkney Islands. The westernmost portion of the study region is typically covered with multi-year pack ice throughout the year, whereas the eastern portion is ice-free in summer (approximately January to March) and partially to completely ice-covered for the remainder of the year (ZWALLY *et al.*, 1983).

Most previous physical oceanographic research in the Weddell Sea has consisted of regional-scale analyses of circulation and water-mass structure based upon relatively widely spaced temperature and salinity data. These analyses, integrated through physical reasoning with the surface wind field, have established the presence of a wind-driven, basin-wide cyclonic gyre in the Weddell Sea (e.g. GORDON *et al.*, 1978, 1981; DEACON, 1979). Our study area is believed to be characterized by a general northward flow, which comprises the western limb of this gyre. The water column is nearly homogeneous, indicating that the currents associated with the gyre are primarily barotropic; the geopotential surface height above the 1000 db level shows only very weak baroclinic surface currents (GORDON *et al.*, 1978). Closure of the wind-driven gyral circulation requires a western boundary current with a northward transport of order 60 Sv, vertically integrated current speeds of about 8 cm s^{-1}, and a current width of about 225 km at 65°S (GORDON *et al.*, 1981).

METHODS

We collected data aboard the R.V. *Melville* and the U.S. Coast Guard icebreaker *Glacier* from 7 to 27 March, 1986. The *Melville* was restricted to open-water locations, while the *Glacier* worked primarily in areas of significant ice cover (Fig. 1). Movement of the ships was co-ordinated so that on two occasions we obtained nearly synoptic east–west transects through the marginal ice zone, with sampling completed in <46 h. One transect crossed the southern portion of the study area from 7 to 9 March (*Melville* Stas 2–10; *Glacier* Stas 1–7), and the second, the northern portion from 25 to 27 March (*Melville* Stas 43–53; *Glacier* Stas 24–28). Each transect was approximately 400 km in length. Additional stations were located along primarily these two main transect lines (Fig. 1). On 4 March a Polar Research Laboratory Argos-tracked buoy was deployed through a hole bored into a large multi-year ice floe (about 200 m in horizontal dimension and 2 m thick) in the extreme southwest corner of the study area (Fig. 1). Several position fixes were obtained per day throughout the month of March.

At each station we collected vertical profile data on temperature, salinity, nutrient concentrations (NO_3^-, NO_2^-, NH_4^+, $Si(OH)_4$ and HPO_4^{2-}), Chl *a*, particulate carbon, nitrogen and biogenic silica. Temperature and salinity data were obtained using a Neil Brown Mark IV CTD system on each ship. We made a total of 115 CTD casts, with nearly all extending to 500 m and more than half to 1500 m. The CTD system aboard *Glacier* was calibrated before and after the cruise at the Northwest Regional Calibration Center (Bellevue, Washington). The *Melville's* system was calibrated at Texas A&M University after the cruise. Temperature and salinity calibrations were obtained about every third cast, using a Niskin bottle and reversing thermometers aboard the *Glacier* and a rosette sampler on the *Melville*. The lowering rate of the CTD was limited to 0.5 m s^{-1} through the upper 150 m to optimize vertical resolution and minimize problems related to sensor lag time (such as spiking through the relatively strong vertical temperature and conductivity gradients present within this depth interval). Simultaneous casts taken when the ships were separated by only a few hundred meters at the start and end of the cruise indicate that the data from the two instruments agree to within 0.01°C and 0.01‰.

We collected 10 l seawater samples at nine depths in the upper 150 m at each station. The upper seven depths corresponded to the approximate depths of 100, 50, 30, 15, 5, 1, and 0.1% of surface irradiance, as estimated from lowerings of a submersible quantum meter and a Secchi disk. The others provided equal sample spacing between the 0.1% isolume and 150 m. Samples from stations occupied at night were taken at depths selected from the most recent daylight station. Samples taken in areas of significant ice cover were collected at depths chosen from the most recent irradiance profile in an open lead or polynya. Each sample was drawn into a 20 l polypropylene carboy fitted with a spigot 2 cm above the bottom. Subsamples for individual analyses were drawn from this carboy. This sampling procedure ensures that rapidly sinking particles are adequately represented in all samples, as the carboys were routinely agitated during subsampling (CALVERT and MCCARTNEY, 1979).

Duplicate samples for nutrient analysis were gently syringe filtered through 0.6 μm pore-size polycarbonate membrane filters (Nuclepore, Inc.), frozen and stored for later analysis. One complete set of frozen samples from both ships were returned to the U.S. on each ship. Maximum–minimum thermometers placed in the freezers aboard both ships confirmed that the samples were returned without thawing. Samples were then thawed in a tepid water bath and analysed on a four-channel, continuous flow colorimetric analyser using methods adapted from those of ATLAS *et al.* (1971). Separate samples for ammonium analyses were filtered in a similar manner and analysed immediately at sea, using a modification of the method of SOLORZANO (1969). Standard deviations for a single analysis were 0.4 μM for nitrate and silicic acid, 0.03 μM for phosphate, 0.013 μM for nitrite and 0.07 μM for ammonium.

Chlorophyll *a* analyses were performed on board by filtering 1.0 l seawater samples through Gelman A/E glass fiber filters. These filters were then homogenized in 90% acetone, extracted and centrifuged. The fluorescence of the extract before and after acidification was measured with a Turner Designs fluorometer which had been calibrated with commercially purified Chl *a* preparations.

Particulate carbon and nitrogen were measured by filtering 1.2 l of seawater through precombusted (450°C for 2 h) Whatman GF/C glass fiber filters. Each filter was rinsed with 5–10 ml of 0.01 N HCl in filtered seawater to remove any inorganic carbonates, then folded, placed in precombusted glass vials, dried at 60°C and returned to the University of Tennessee for analysis on a Perkin-Elmer model 240B elemental analyser. Corrections for absorption of dissolved organic carbon and nitrogen by the filter were made by subtracting values from a second filter placed beneath the primary filter and processed identically. These corrections were typically small, but not negligible; e.g. they averaged 6.7% for nitrogen. Approximate limits of detection were 0.5 and 0.1 μmol l^{-1} for carbon and nitrogen, respectively.

Samples (1.2 l) for analysis of biogenic particulate silica were vacuum filtered through 0.6 μm Nuclepore filters which were then folded, dried at 60°C in covered plastic Petri dishes and returned to Oregon State University for analysis. Biogenic silica was dissolved by NaOH digestion (Paasche, 1973), and the resulting solution analysed for dissolved reactive silicate by the acid-molybdate method of Strickland and Parsons (1972). To maximize sensitivity the sample and reagent volumes were reduced so that 4.0 ml of acidified molybdate solution and then 6.0 ml of metol/sulfite reducing reagent were added to neutralized digestion solutions whose volume was 10 ml. Absorbance at 810 nm was measured in low-volume (*ca* 9 ml) 10 cm spectrophotometer cells (Hellma, Inc.). Analysis of reagent blanks, filter blanks and low-level standards in our laboratory indicates an analytical precision of ±5% and a detection limit of 10–15 nmol l^{-1} for this method.

Bacteria were enumerated by DAPI (4,6,6-diamidino-2-phenylindole 2 HCl, Sigma) stained specimens collected on 0.2 μm pore size Nuclepore filters, as described by Grossi *et al.* (1984). Direct counts were performed using a Zeiss research microscope equipped with an ultraviolet light source (HBO Osram, 50W) and appropriate filters. Bacterial biovolumes were estimated from cell dimensions (Zimmerman, 1977) and carbon biomass derived from biovolume using a conversion factor of 18.3 fmol C μm^{-3} (Bratbak and Dundas, 1984).

RESULTS

The edge of the pack ice was sharply defined within the study area in March 1986, with the entire transition from open water to >80% ice cover generally occurring within 10 km or less (Fig. 1). Also, the ice edge maintained an almost stationary position throughout our 3 week sampling period. Both of these properties of the ice frontal zone were very different from those we had observed in the Weddell–Scotia Sea during austral spring, when the ice-cover gradient was much more diffuse and the entire ice-edge system was retreating southward at a mean rate of >5 km day^{-1} (Comiso and Sullivan, 1986).

The upper water column was well stratified in salinity and density throughout the study area (Fig. 2). There was an upper mixed layer 30–50 m deep at every station occupied. Temperature in this layer varied from freezing (about –1.83°C) beneath the ice to warmer than –0.5°C toward the eastern end of the study region. Surface salinity was between 33.3 and 33.9‰, with the lower values in the more northerly section and underlying the ice edge. A sharp halocline and resulting pynocline underlay the upper mixed layer, with salinities increasing to about 34.4‰ at approximately 50 m. Salinity increased gradually with depth below this halocline. In contrast to the vertical salinity distribution, temperature in the open-water portion of the study area was lowest in a layer centered at about 80 m, in which temperatures were colder than –1.5°C. Temperature increased with depth below this layer, with the strongest gradients between 100 and 200 m. The upper mixed layer comprises the Weddell Surface Water layer, which varies seasonally in its temperature and salinity characteristics. The underlying cold core is the Weddell Winter Water, a remnant from the preceding winter's cold convective layer. Beneath the Winter Water, temperature and salinity increase with depth in the upper portion of the Weddell Warm Deep layer. A statistically rigorous discussion of these water types has been presented by Carmack (1977).

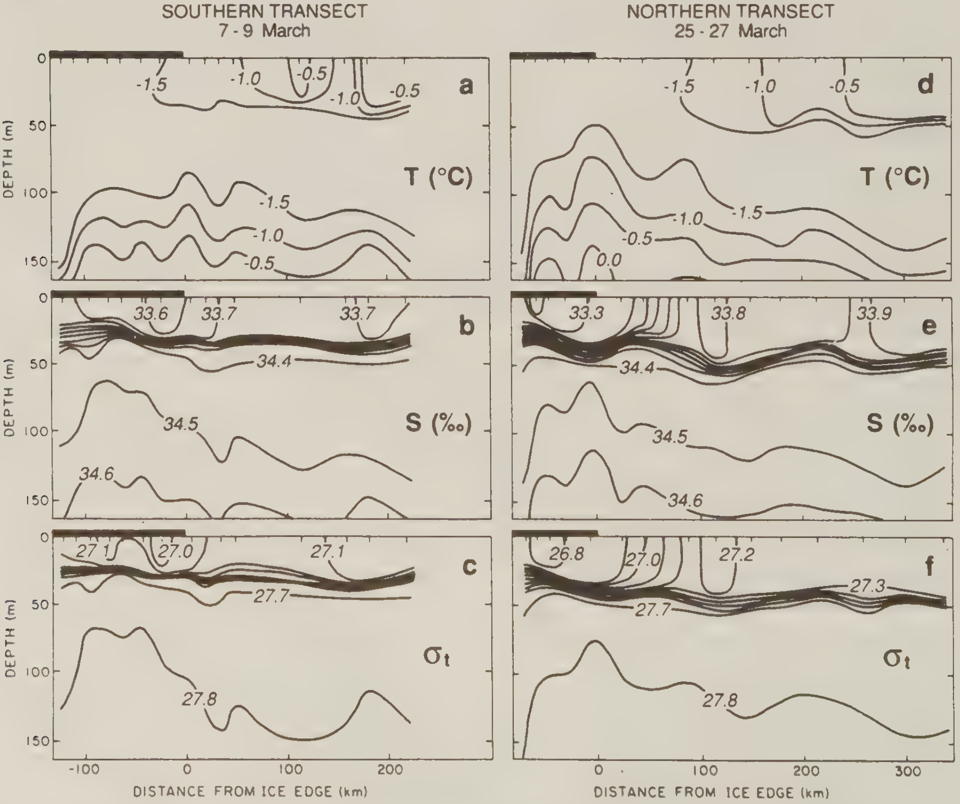


Fig. 2. Distributions of temperature, salinity and density (σ_t) in the upper 150 m along the quasi-synoptic transects occupied on 7–9 March (a–c) and 25–27 March (d–f). The bar in the upper left of each panel denotes heavy (>80%) ice cover.

The dynamic topography of the surface relative to 500 db indicates that baroclinic circulation of the upper 500 m was confined to a barely significant eastward, then northward, surface drift in the western portion of the study area (Fig. 3). The surface dynamic topography relative to 1500 db (not shown) exhibits virtually the same pattern. These observations are consistent with past conclusions that the regional flow is primarily barotropic. The large multi-year ice floe which was instrumented for drift measurements near the start of the field program showed almost no net meridional drift and little net zonal drift during March (British Antarctic Survey, unpublished data).

The gross features of the vertical distributions of temperature and salinity did not appear to change significantly during March, as seen by comparing distributions early and late in the cruise (Fig. 2). The later, more northerly section showed lower salinities in the upper layer and a somewhat deeper upper mixed layer than the earlier southern transect. Air temperatures were sub-freezing for all but 4 days of the cruise, and the ice edge was in water colder than –1.0°C, so it is unlikely that significant melting occurred during March. The location of the ice edge, as monitored both from the cruise vessels and by the Navy–NOAA ice forecast center using satellite data, remained effectively unchanged throughout the study, consistent with the absence of either net melting or net freezing. It is likely that the depressed salinities farther north represented a remnant of previous meltwater accumulation along the ice edge. Little variation occurred below the Surface Water layer, as temperature and salinity remained unchanged during the course of our observations. An elevation of the isohalines (and isopycnals) in the vicinity of the ice edge persisted through the cruise. While this feature may suggest upwelling, surface winds during the cruise were neither persistent enough nor in the proper direction to induce upwelling.

There was a consistent maximum in phytoplankton biomass centered about 150 km seaward of the ice edge (Figs 4a–d and 5a–c). Phytoplankton biomass maxima often have been observed in open water 50–200 km seaward of the ice edge in other areas (e.g. Alexander and Niebauer, 1981; Smith and Nelson, 1985; Nelson *et al.*, 1987). However, these previous studies have shown a high degree of spatial correlation, both vertically and laterally, between elevated phytoplankton biomass and low-salinity surface

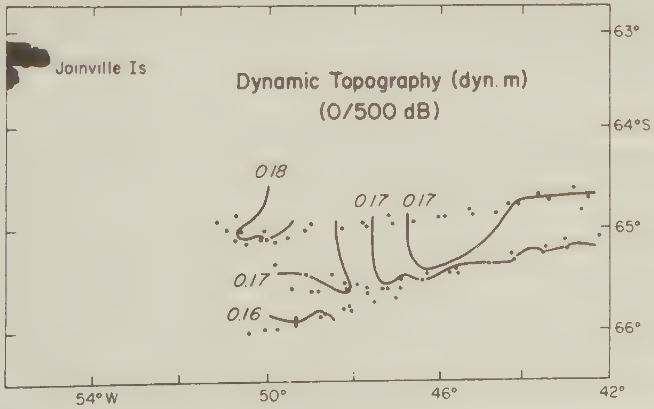


Fig. 3. Dynamic topography (in dyn m) relative to the 500 dB surface within the study area. Almost no mean baroclinic flow is detectable.

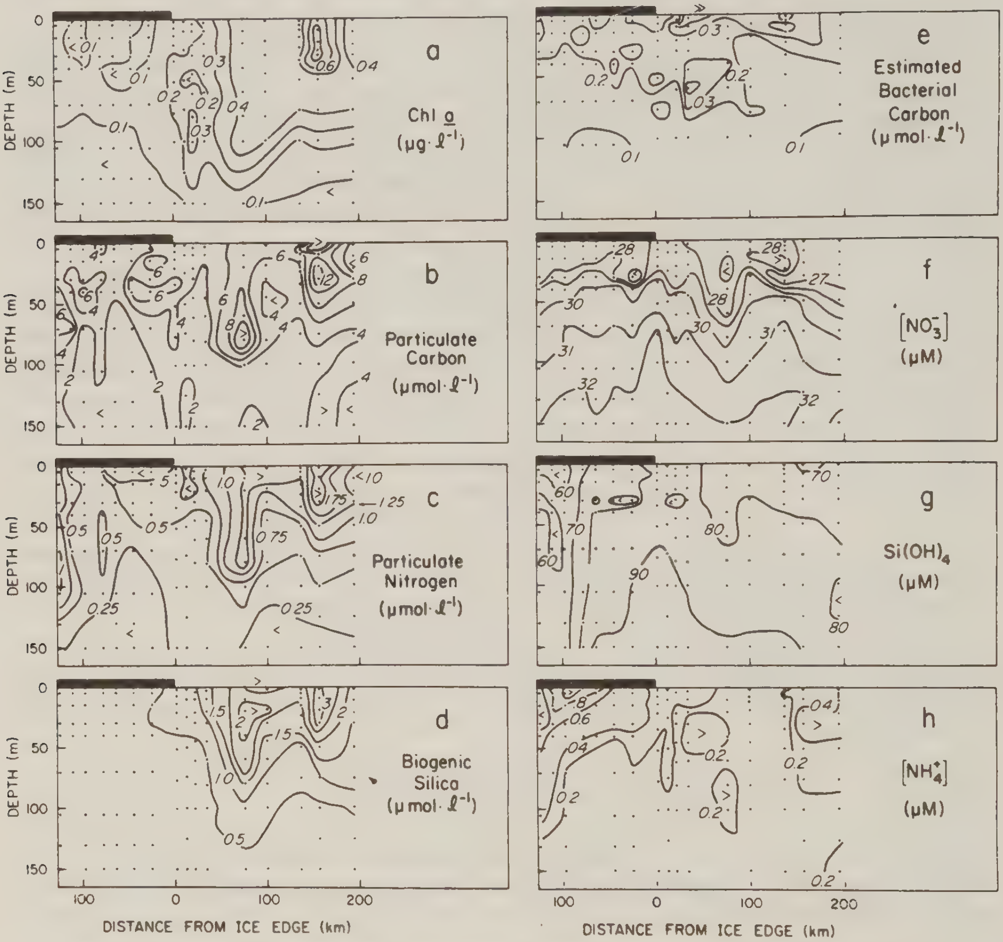


Fig. 4. Sections of phytoplankton biomass and nutrient concentrations in the upper 150 m along the transect across the southern portion of the study area, 7–9 March. (a) Chl *a*; (b) particulate carbon; (c) particulate nitrogen; (d) biogenic silica; (e) estimated bacterial carbon; (f) nitrate; (g) silicic acid; (h) ammonium. The bar in the upper left of each panel denotes heavy (>80%) ice cover.

water derived from ice melt. This was not the case in the Weddell Sea ice-edge zone during March 1986. All phytoplankton biomass parameters showed distinct mesoscale maxima 100–150 km in iceward-seaward extent (Figs 4a–d and 5a–c), while the hydrographic structure of the upper 100 m was dominated by a strong halocline/pycnocline at 30–50 m that was present throughout the ice-edge region and whose depth and intensity were nearly uniform laterally (see Fig. 2). In addition, all phytoplankton biomass parameters show distributions in which high biomass was not restricted to the stable surface layer, but instead penetrated into and through the main pycnocline.

There were two distinct relationships between the biogenic particle fields and the ice edge itself: the two biomass parameters whose only significant source is phytoplankton growth (i.e. Chl *a* and biogenic silica), decreased to very low levels at the ice edge and

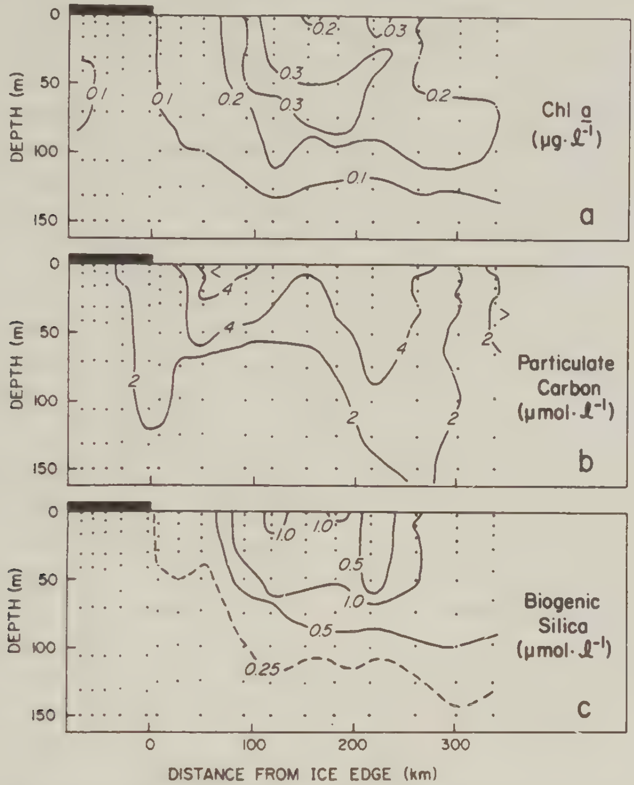


Fig. 5. Sections of selected phytoplankton biomass parameters in the upper 150 m along the transect across the northern portion of the study area, 25–27 March. (a) Chl *a*; (b) particulate carbon; (c) biogenic silica.

remained low throughout the ice-covered portion of the system (Figs 4a, d and 5a, c). In contrast, particulate carbon and nitrogen, which include both autotrophic and heterotrophic biomass as well as any organic detritus, did not decrease sharply at the ice edge and at times exhibited maxima in ice-covered waters (Figs 4b, c and 5b).

Chlorophyll *a* concentrations seldom exceeded 0.7 μg l^{-1}, even in the core of the phytoplankton biomass maximum. Many previous studies of phytoplankton in ice-edge regions have reported Chl *a* concentrations >5 μg l^{-1}, with occasional values >20 μg l^{-1} (e.g. Alexander and Niebauer, 1981; Smith *et al.*, 1985; Smith and Nelson, 1985; Nelson *et al.*, 1987). We have previously reported the spatial dimensions of ice-edge phytoplankton blooms in the Southern Ocean by defining "bloom" chlorophyll concentrations as those exceeding 1.0 μg l^{-1} (Nelson and Smith, 1986; Nelson *et al.*, 1987). By that definition, the much less intense maximum in Chl *a* observed in the ice-edge region during March 1986 was not strong enough to be characterized as a phytoplankton bloom.

In contrast to the relatively low Chl *a* levels, the highest particulate carbon concentrations exceeded 10 μmol l^{-1} (Fig. 4b). These values are about half as high as those measured within a fairly intense (Chl a > 5 μg l^{-1}) ice-edge bloom in the Weddell–Scotia Sea in the spring of 1983 (Nelson *et al.*, 1987). Biogenic silica concentrations were generally >1.5 μmol l^{-1} and occasionally >3.5 μmol l^{-1} within the biomass maximum sampled in March (Fig. 4d). These values actually exceeded those measured in the spring 1983 ice-edge bloom (Nelson *et al.*, 1987).

Bacterial biomass generally decreased with depth, and the bacterial carbon distribution was similar to that of all phytoplankton biomass parameters in that high values penetrated well into, and beneath, the main pycnocline (Fig. 4e). However, unlike Chl *a* and biogenic silica, bacterial carbon was quite high in the surface layer in ice-covered waters. The estimated bacterial carbon concentrations (generally 0.2–0.4 μmol l^{-1}) ranged from about 2 to 10% of the total particulate carbon.

The phytoplankton biomass maximum was associated with localized minima in the concentrations of nitrate and silicic acid (Fig. 4f, g) as well as phosphate (not shown). This spatial correlation between phytoplankton maxima and nutrient minima is quite common in marginal ice zones of both northern and southern polar oceans (e.g. Smith *et al.*, 1985; Nelson and Smith, 1986; Nelson *et al.*, 1987) and indicates that the nutrient field is affected strongly by *in situ* uptake by phytoplankton. Most significantly, the high-biomass waters within and beneath the pycnocline also exhibited nitrate and silicic acid minima (Fig. 4). Since the temperature and salinity sections provide no evidence of vertical mixing through the pycnocline in these areas (Fig. 2), the nutrient sections suggest that active uptake of nitrate, phosphate and silicic acid by the phytoplankton extended through the pycnocline to at least 75 m, and perhaps deeper, in high-biomass areas seaward of the ice edge.

Surface waters were consistently richer in ammonium than were subsurface waters, both under the ice and in open-water areas (Fig. 4h). Maximum concentrations (0.8–0.9 μM) occurred under the ice, whereas open-water stations exhibited ammonium concentrations no higher than 0.6 μM. None of the ammonium concentrations measured approached those observed in subsurface maxima in the Ross Sea (Biggs, 1982) or the Fram Strait marginal ice zone (Smith *et al.*, 1985).

DISCUSSION

Physical conditions

During March 1986 the area we examined in the western Weddell Sea was characterized by negligible baroclinic circulation. The ice floe that had been instrumented so that its motion could be tracked using the Argos system was almost motionless through this period, suggesting that total as well as baroclinic flow was small. Gordon *et al.* (1981) suggested a hypothetical western boundary current, flowing northward along the Antarctic Peninsula, in order to close the cyclonic circulation in the Weddell Gyre. Their computed width for this boundary current was 225 km. Assuming that those computations are correct, our data, collected 100–500 km east of the continental slope of the Antarctic Peninsula, would have included the eastern portion of this current. It is difficult to reconcile the very weak observed circulation with the concept of a western boundary current, and it may be that the actual current is narrower or has lower speeds, at least in late summer.

A lack of significant current activity in the study area is consistent with the observed vertical temperature and salinity structure. Small steps (on the order of meters in vertical scale) occurred at all stations in the upper Warm Deep Water layer from about 100 to 180 m (Husby and Muench, 1988). Similar features have been reported for the same general area by MIDDLETON and FOSTER (1980), who attributed them to double-diffusive processes. Below about 180 m, nearly half of the stations showed temperature and salinity steps with vertical scales exceeding 100 m. These also were reported for the Weddell Sea further east by FOSTER and CARMACK (1976), who attributed them to a combination of double diffusion and the cabelling instability. The widespread occurrence and persistence of such features suggest that lateral current shear and related turbulent mixing are small, and that the distributions of temperature and salinity may be controlled primarily by vertical, rather than horizontal processes.

The hydrographic structure of the upper layers near the ice edge was more uniform horizontally than has been observed in other ice-edge regions. The Bering Sea and Greenland Sea ice edges are accompanied by major oceanic frontal structures (MUENCH and SCHUMACHER, 1985; PAQUETTE *et al.*, 1985). The spring Weddell–Scotia Sea ice edge was associated with large mesoscale lateral variations in water characteristics (NELSON *et al.*, 1987). In each of these cases, the lateral variations were strongly influenced by regional oceanic circulation features. For example, the East Greenland Sea ice edge coincides with the East Greenland Polar Front, a mesoscale ocean circulation feature which interacts with, and exerts a strong control over, the ice edge. The complexity of the Weddell–Scotia Sea ice edge is forced by mesoscale oceanic features associated with the strong currents through the Drake Passage. No such features were observed in the northwestern Weddell Sea. The upper mixed layer extended, with little variation in depth, from well beneath the ice to more than 300 km seaward of the ice edge. Low salinity fronts within this layer (Fig. 2) may have been associated with localized circulations, but these features were not studied in detail.

Biomass distributions

When the particulate matter distributions in the two sections are compared, the overall spatial patterns of all parameters are similar (i.e. maxima seaward of the ice edge and a decrease under the ice; see Figs 4 and 5). However the first, and more southerly, transect exhibited maximum levels of all biomass parameters about twice as high as those observed on the second. The first transect (Fig. 4) was sampled 2–3 weeks earlier, and was about 80 km farther south, than the second. It is possible that the differences we observed between the two transects resulted from biological removal processes that were degrading the bloom with time. However, EL-SAYED and TAGUCHI (1981) have found marked north–south trends in productivity and biomass in the Weddell Sea, over distances of several hundred km. A similar meridional distribution of biomass appears to have existed during the time of our study. Satellite ocean-color data show that the ice-edge phytoplankton biomass maximum we observed between 64° and 65°30′S extended southward to approximately 72°S and exhibited its highest chlorophyll concentrations well to the south of our study area (COMISO *et al.*, 1987). Data on vertically integrated Chl *a* within our study area also provide some indication of a north–south gradient in phytoplankton biomass that persisted through March (Fig. 6). Considering this meridional biomass gradient in the context of the larger-scale synoptic view provided by satellite data suggests that our study area was located near the northern limit of an extensive ice-edge phytoplankton bloom that was significantly more intense 300–800 km to the south.

The observed lack of close correlation, either vertically or horizontally, between the upper-layer density structure and the distribution of biogenic particulate matter was unexpected, and differs sharply from previous observations. In most earlier studies of marginal ice zones, any observed increase in phytoplankton biomass was strongly related to vertical stratification (e.g. Alexander and Niebauer, 1981; Smith and Nelson, 1985), although in some situations the previous light regime of the water masses at the ice edge (Nelson *et al.*, 1987) or nutrient concentrations (Smith *et al.*, 1985) also had influenced the development of the ice-edge bloom. In the Southern Ocean, where nutrients are almost always present at non-limiting concentrations, vertical stability has been implicated as the major factor in controlling primary productivity (e.g. Sakshaug and Holm-Hansen, 1984; Smith and Nelson, 1986). In March of 1986 the entire marginal ice zone of the northwestern Weddell Sea exhibited strong vertical stability in the upper 30–50 m, and all measured nutrient concentrations were high enough to have supported vigorous phytoplankton growth. A phytoplankton biomass maximum was present, but was both less intense and less correlated spatially with the physical structure than has been the case in ice-edge phytoplankton blooms at other times of year. This implies that some factor other than vertical stability and nutrient availability was playing a major role in limiting the intensity and spatial extent of the bloom. Possibilities include:

Light limitation. Total daily irradiance in March ranged from 5.8 to 41 Ein m^{-2} day^{-1}, with a mean of 16.0. This is considerably less light than has been measured in other ice-edge regions during phytoplankton blooms. For example, the mean integrated daily irradiance in the Weddell–Scotia Sea during November 1983 was 25.7 Ein m^{-2} day^{-1}, and that in the western Ross Sea during late January/early February 1983 was approximately 70. SooHoo *et al.* (1987) reported spectral irradiance data and photosynthesis vs irradiance response curves which suggest that phytoplankton photosynthetic rates were limited by light through 20–80% of the euphotic zone in our study area. Thus it is possible that the magnitude of the bloom we observed was limited by light availability. However, light limitation provides no obvious explanation of the lack of spatial correlation between phytoplankton biomass and vertical stability (Figs 2 and 4) or for the appearance of large ice-edge blooms well to the south of our study area (Comiso *et al.*, 1987).

Micronutrient availability. While biologically utilizable forms of nitrogen, phosphorous and silicon were present in high concentrations in the surface layer throughout the study area, the concentrations and chemical speciation of trace metals and other potentially limiting micronutrients were not measured. Recently, particular emphasis has been given to the possibility of iron limitation in the Southern Ocean, because of the absence of identifiable sources of iron to the water column (Martin and Fitzwater, 1988). A strongly stratified surface layer, late in the productive season, may be an excellent place to find depletion of iron or other micronutrients to levels that limit phytoplankton growth if limitation of this sort does in fact occur in the ice-edge zone.

Grazing or other removal processes. It is possible that the Weddell Sea ice-edge zone in March 1986 was no less favorable an environment for phytoplankton growth than were other marginal ice-zone systems that exhibited high phytoplankton biomass. Biomass-specific rates of ^{14}C and ^{15}N uptake by phytoplankton in our study area (Smith and Nelson, 1987; Nelson and Smith, 1987) were comparable to those in more intense phytoplankton blooms, lending support to the idea that this area was characterized by phytoplankton growth no less vigorous than that occurring in ice-edge zones in spring and summer. If this is the case, then the lower biomass levels may have resulted from intensified grazing pressure or other removal processes. Standing stocks of most herbivorous macrozooplankton appear to have been too low to exert major control over the phytoplankton biomass (Hopkins and Torres, in press), but microzooplankton biomass ranged from about 20 to 60% of the estimated phytoplankton biomass and showed a positive spatial correlation with Chl *a* (Garrison and Buck, 1987). This estimated ratio of microzooplankton biomass to phytoplankton biomass is about four times as high as that observed in the spring 1983 ice-edge bloom in the Weddell–Scotia Sea (Garrison and Buck, 1987), so it is likely that grazing by microzooplankton played a greater role in controlling phytoplankton biomass in the ice-edge zone during March 1986 than has been the case in some other ice-edge systems.

Another possible removal term is grazing by krill; net tows and acoustic sampling during our cruise provide no evidence of high krill abundance in open-water areas of the northwestern Weddell Sea during March (Daly *et al.*, 1987), yet gut-content analysis of seals and seabirds in the study region indicates that krill comprised a major portion of the diet of these very abundant carnivores (e.g. Ainley *et al.*, in press). Clearly the use of krill as a major food item does not necessarily imply high krill stocks. Nonetheless, the direct and indirect sampling methods do lead to somewhat different conclusions regarding the abundance of krill within the study area. Juvenile krill were observed in high abundance on the under surface of ice floes (Daly *et al.*, 1987), and it is possible that the combination of large standing stocks of krill and low phytoplankton biomass resulted in the ammonium concentration maximum observed under the ice (Fig. 4h). If krill also were present in high concentrations seaward of the ice edge, they could have exerted significant control on the phytoplankton biomass.

We cannot assess any one of these possibilities in detail on the basis of data collected in 1986. It appears, however, that some factor, or combination of factors, other than water-column stability and macronutrient availability was instrumental in controlling both the spatial distribution and the overall level of phytoplankton biomass in the ice-edge zone of the northwestern Weddell Sea during the late summer/early autumn of 1986.

Particulate matter composition

The biogenic particle field we sampled in March was very different in its chemical composition from that observed in the Weddell–Scotia Sea during the austral spring (Nelson *et al.*, 1987). In that system, Chl *a* concentrations were about an order of magnitude higher than those reported here, particulate carbon and nitrogen about twice as high, and biogenic silica nearly the same. The elemental ratios and carbon:chlorophyll ratios observed in spring were similar to those of compositionally normal phytoplankton (Nelson *et al.*, 1987). The ratios encountered during this study (Table 1) were highly unusual for particulate matter in the oceanic surface layer, but similar to those observed in the ice-edge zone of the western Ross Sea during January–February 1983 (Smith and Nelson, 1985). During that study the bloom was very dense, with all biomass parameters approximately 10 times higher than those we report here. The high overall biomass levels within the Ross Sea bloom and the anomalous composition of that material combined to produce biogenic silica concentrations greater by a factor of three than any which had been observed previously in surface seawater (Nelson and Smith, 1986). If the compositional ratios reported here are not greatly biased by detrital material, this is the second reported observation of a biomass maximum in the marginal ice zone of the Southern Ocean that is unusually rich in organic carbon and exceptionally rich in biogenic silica per unit chlorophyll. These direct observations of biogenic particulate matter that is rich in silica are consistent with previously reported large-scale patterns of vertical nutrient

Table 1. Mean values of selected phytoplankton biomass parameters in three marginal ice zones of the Southern Ocean

Parameter	Weddell–Scotia Sea November 1983[*]	Western Ross Sea January–February 1983[†]	Western Weddell Sea March 1986[‡]
Chlorophyll *a* (µg l^{-1})	4.0	2.9	0.38
Particulate carbon (µmol l^{-1})	10.6	33.2	3.6
Particulate nitrogen (µmol l^{-1})	1.5	5.6	0.46
Biogenic silica (µmol l^{-1})	1.4	21.7	1.6
Carbon:chlorophyll mass ratio	31.8	138	114
Carbon:nitrogen mole ratio	7.1	5.9	7.8
Silica:carbon mole ratio	0.13	0.65	0.44

[*] Data from Nelson *et al.* (1987).

[†] Data from Nelson and Smith (1986).

[‡] Present study; The data set includes all values from the surface to the 1% light depth at locations seaward of the ice edge.

concentration gradients in the upper ocean, which suggest that the Southern Ocean is the only geographically extensive region in which the net removal of silicic acid from the surface layer significantly exceeds that of nitrate (Kamykowski and Zentara, 1985). High ratios of biogenic silica to organic carbon in the phytoplankton also may help explain the observation that the Southern Ocean exhibits very high accumulation rates of siliceous sediments (DeMaster, 1981; Ledford-Hoffman *et al.*, 1986) in spite of relatively low photosynthetic productivity (Holm-Hansen *et al.*, 1977; Smith and Nelson, 1986).

In the Ross Sea ice-edge bloom very little organic or siliceous detritus was observed microscopically (Smith and Nelson, 1985), ^{14}C autoradiography indicated that nearly all physically intact cells were photosynthetically active (Wilson *et al.*, 1986), and the relative uptake rates of carbon, nitrogen and silicon closely parallelled the observed, highly anomalous, elemental ratios of the suspended particle assemblage (Nelson and Smith, 1986). These lines of evidence all suggest that the unusual elemental composition of the suspended particulate matter reflected the composition of the phytoplankton rather than a detrital influence. In the present study we have less evidence on the relative proportions of living and detrital particulate matter. Bacterial biomass made only a small (2–10%) contribution to the total particulate carbon pool (Fig. 4b, e), but protozoan microzooplankton biomass may have comprised up to 30% of the total suspended particulate carbon at some stations (Garrison and Buck, 1987). Carbon: nitrogen ratios were similar to those observed in phytoplankton cultures growing vigorously with excess nitrate (Parsons *et al.*, 1984), implying that living phytoplankton comprised a high fraction of the particulate organic matter. Finally, microscopic examination of preserved whole water samples did not indicate large amounts of either organic or siliceous detrital material, and cell counts from selected stations within the bloom indicate that the diatom *Dactyliosolen tenuijunctus* dominated the phytoplankton assemblage, both numerically and on a biovolume basis (K. R. Buck, personal communication). This diatom was observed to have very little of the volume within the frustule occupied by photoplasm and to contain very little autofluorescent material, including Chl *a*. This cell structure of a dominant diatom within the study area is consistent with our measurements of high biogenic silica levels per unit Chl *a*. From the several lines of evidence detailed above we conclude that the particulate matter within the biomass

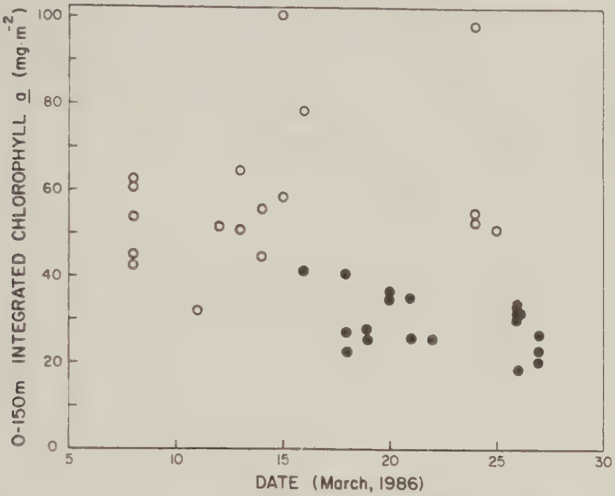


Fig. 6. Integrated Chl *a* content of the upper 150 m at open-water locations, as a function of time during March 1986. Open circles denote stations occupied along the more southerly transect line; solid circles represent stations along the more northerly line. The mean Chl *a* content for all southerly stations was 50.7 mg m^{-2} (S.D. = 22.6) while the mean for all northerly stations was 26.9 mg m^{-2} (S.D. = 8.2).

maximum probably consisted mostly of living phytoplankton cells, with a smaller but significant fraction of living microzooplankton, and that the phytoplankton was unusually rich in silica in comparison with its organic matter and pigment content.

The approximate amount of detrital particulate material can be estimated in two other ways. Figure 7 presents the vertically integrated particulate carbon and biogenic silica content of the upper 150 m, plotted as a function of vertically integrated Chl *a*. When the regressions are done point-by-point on data from individual depths rather than using vertically integrated biomass, the relationships are similar (Table 2). We have illustrated the integral regressions in Fig. 7 because the very large number of data points from individual depths result in dense clouds of points from which individual values cannot be discerned. To a first approximation the value of the *y*-intercept in these regressions is an estimate of the amount of detrital, or at least non-chlorophyllous, organic or siliceous material present at stations exhibiting low Chl *a* concentrations and the slope of the regression line estimates the carbon:Chl *a* or silica:Chl *a* ratio of the phytoplankton assemblage. The *y*-intercept of 217 μmol C m^{-2} for vertically integrated data implies an average of about 1.5 μmol l^{-1} detrital C in the upper 150 m. Biogenic silica shows a higher degree of spatial correlation with Chl *a* than does POC in both the point-by-point and station-by-station regressions (Table 2), and in both cases the *y*-intercept for biogenic silica is statistically indistinguishable from zero. This tends to confirm the conclusion derived from microscopic examination that there was very little detrital siliceous material in the study area. Taken together, these regressions suggest that the silica:carbon mole ratio of the living material (i.e. after correcting for detrital carbon) was at least (4.15/8.07) or 0.51. This is four times as high as the mean silica:carbon ratio found for diatoms in nutrient-replete cultures (BRZEZINSKI, 1985) and comparable to the very high ratio observed in the Ross Sea (SMITH and NELSON, 1985). Thus these regressions suggest a

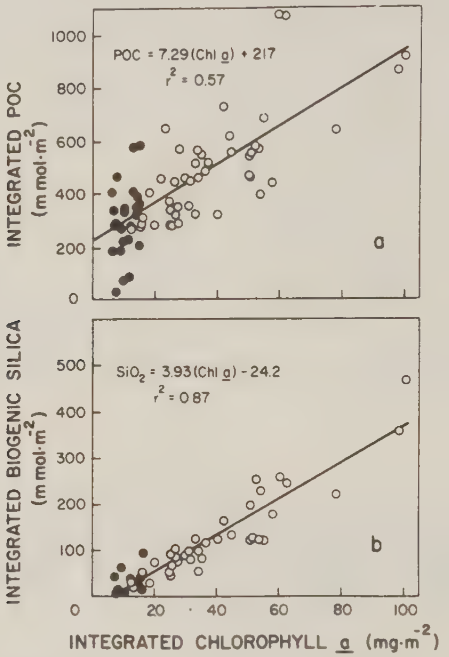


Fig. 7. Integrated particulate organic carbon (a) and biogenic silica (b) content of the upper 150 m, as a function of vertically integrated Chl *a*. Closed circles represent ice-covered locations, open circles areas with little or no ice cover. Linear regression lines (see Table 2) are also shown.

Table 2. Statistical parameters of linear regressions of particulate organic carbon and biogenic silica vs Chl a *in the ice-edge zone of the northwestern Weddell Sea during March* 1986

	Particulate organic carbon	Biogenic silica
(a) From regression of individual data points:		
Slope (mol g Chl a^{-1})	8.07	4.15
Equivalent mass ratio	96.8	249
Intercept at zero Chl *a* (μmol l^{-1})	1.70	−0.12
Correlation coefficient (r^2)	0.55	0.81
(b) From regression of vertically integrated data:		
Slope (mol g Chl a^{-1})	7.29	3.93
Equivalent mass ratio	87.5	236
Intercept at zero Chl *a* (mmol m^{-2})	217	−24.2
Correlation coefficient (r^2)	0.57	0.87

minimum detrital carbon value on the order of 1.5 μmol l^{-1}, negligible siliceous detritus and living phytoplankton with unusually high carbon:chlorophyll and silica:carbon ratios.

A second estimate of detrital carbon can be made by summing the estimated carbon content of the identified biomass pools that would be collected by a 10 l sampling bottle (phytoplankton, microzooplankton and bacteria) and subtracting that total from the measured particulate carbon concentration (Robinson *et al.*, 1987). These estimates of detrital carbon range from 1.2 to 3.3 μmol l^{-1}, in reasonably good agreement with the >1.5 μmol l^{-1} estimate derived from the carbon:Chl *a* regressions. The organic carbon mass-balance approach also indicates that the amount of detrital organic material varied much less with distance from the ice edge than did phytoplankton biomass. Thus detritus appears to have been a major component of the suspended particle assemblage beneath the ice and for several kilometers seaward of the ice edge but the biomass maximum centred 50–150 km seaward of the ice edge contained a much higher fraction of living material.

Seasonal duration of ice-edge phytoplankton blooms

The growing body of data on phytoplankton biomass in the marginal ice zone of the Southern Ocean indicates that ice-edge blooms are quite common spatially and quite persistent seasonally. Two previous sets of observations from the Weddell Sea have indicated that such blooms begin no later than October or November (JENNINGS *et al.*, 1984; NELSON *et al.*, 1987), and data reported here show elevated biomass levels in the ice-edge zone through late March. If this is generally true, then ice-edge blooms persist much later into the summer/autumn season than does active retreat of the ice edge. Ice-edge phytoplankton blooms may have even greater seasonal duration than these data indicate. Preliminary observations from the eastern Weddell Sea aboard the F.S. *Polarstern* in 1986 have shown elevated chlorophyll levels in the ice-edge region during late August (DIECKMANN, 1987), a time of year when the ice edge in the Weddell Sea is at its northern limit (*ca* 58°S) and thus receiving much more light than would be the case at more poleward locations. Those observations combine with ours to show that there are at least some areas of elevated phytoplankton biomass in the marginal ice zone of the Southern Ocean from at least late August to late March, a much longer time than has been considered in seasonal productivity estimates for the Southern Ocean. Thus, recent estimates of the importance of ice-edge blooms in the overall annual productivity of the Southern Ocean (SMITH and NELSON, 1986; SMITH *et al.*, in press) must be conservative because they consider only retreating ice edges. Since these estimates attribute 35–50% of the total annual primary productivity of the Southern Ocean to phytoplankton blooms in the ice-edge regions, our observation of elevated biomass persisting through March underscores the major quantitative importance of the ice-edge region in the ecological and biogeochemical cycles of the Southern Ocean.

Acknowledgements—We thank Julie A. Ahern, Nancy K. Keene, Steven T. Kottmeier, Stanley A. Moore, David L. Wilson and Robert Wilson for their assistance during the seagoing phase of this study. Julie Ahern also performed much of the post-cruise analytical and data-processing work, as did Haifa Harb, Joe C. Jennings, Jr, Jacque Johnson, Dale H. Robinson, and Kean Stump. David MacDonald (Texas A&M University) assisted in the calibration of the CTD units. Kurt R. Buck and David L. Garrison (University of California, Santa Cruz) and Kendra L. Daly (University of Washington) provided us with unpublished data that helped us greatly in interpreting our results, and also provided valuable comments on earlier versions of this paper. This work was supported by National Science Foundation grants DPP-8420204 to Oregon State University, DPP-8420213 to the University of Tennessee, DPP-8444783 to the University of Southern California, and DPP-8420646 to Science Applications International Corporation and by Office of Naval Research contract N00014-82-C-0064 to S.A.I.C.

REFERENCES

AINLEY D. G., W. R. FRASER, C. W. SULLIVAN, J. J. TORRES, T. L. HOPKINS and W. O. SMITH (1986) Antarctic mesopelagic micronekton: evidence from seabirds that pack ice affects community structure. *Science*, **232**, 847–849.

AINLEY D. G., W. R. FRASER and K. L. DALY (in press) Effect of pack ice on the composition of micronektonic communities in the Weddell Sea. In: *Antarctic Ocean and resources variability*, S. SAHRHAGE, editor, Springer-Verlag, Berlin.

ALEXANDER V. and H. J. NIEBAUER (1981) Oceanography of the Bering Sea ice edge zone in spring. *Limnology and Oceanography*, **26**, 1111–1125.

ATLAS E. L., S. W. HAGER, L. I. GORDON and P. K. PARK (1971) A practical manual for use of the Technicon AutoAnalyzer in seawater nutrient analyses, Technical Report 215, Ref. 71-22, Department of Oceanography, Oregon State University, Corvallis.

BIGGS D. C. (1982) Zooplankton excretion and NH_4^+ cycling in near-surface waters of the Southern Ocean. I. Ross Sea, austral summer, 1977–1978. *Polar Biology*, **1**, 55–67.

BRATBAK G. and S. DUNDAS (1984) Bacterial dry matter content and biomass estimations. *Applied and Environmental Microbiology*, **48**, 755–757.

BRZEZINSKI M. A. (1985) The Si:C:N ratio of marine diatoms: Interspecific variability and the effect of some environmental variables. *Journal of Phycology*, **21**, 347–357.

CALVERT S. E. and M. J. MCCARTNEY (1979) The effect of incomplete recovery of large particles from water samplers on the chemical composition of oceanic particulate matter. *Limnology and Oceanography*, **24**, 523–536.

CARMACK E. C. (1977) Water characteristics of the Southern Ocean south of the Polar Front. In: *A voyage of Discovery*, M. ANGEL, editor, Pergamon Press, New York, pp. 15–41.

COMISO J. C. and C. W. SULLIVAN (1986) Satellite microwave observations of the Weddell Sea ice cover and its marginal ice zone. *Journal of Geophysical Research*, **91**, 9663–9681.

COMISO J. L., C. R. MCCLAIN, C. W. SULLIVAN and W. O. SMITH (1987) Summer sea ice conditions and productivity in the Weddell Sea. *EOS*, **68**, 1708.

DALY K. L., M. MACAULAY and B. FROST (1987) Distribution and abundance of *Euphausia superba* in relation to the Antarctic ice edge. EOS, **68**, 1709.

DEACON G. E. R. (1979) The Weddell Gyre. *Deep-Sea Research*, **26**, 981–995.

DEMASTER D. J. (1981) The supply and accumulation of silica in the marine environment. *Geochimica et Cosmochimica Acta*, **45**, 1715–1732.

DIECKMANN G. (1987) High phytoplankton biomass at the advancing ice edge in the northern Weddell Sea in winter. EOS, **68**, 1765.

EL-SAYED S. Z. and S. TAGUCHI (1981) Primary production and the standing crop of phytoplankton along the ice-edge in the Weddell Sea. *Deep-Sea Research*, **28**, 1017–1032.

FOSTER T. D. and E. C. CARMACK (1976) Temperature and salinity structure in the Weddell Sea. *Journal of Physical Oceanography*, **6**, 36–44.

GARRISON D. L. and K. R. BUCK (1987) Microzooplankton in the ice-edge zone of the Weddell Sea: an AMERIEZ study. EOS, **68**, 1708–1709.

GORDON A. L., E. MOLINELLI and T. BAKER (1978) Large-scale relative dynamic topography of the Southern Ocean. *Journal of Geophysical Research*, **83**, 3023–3032.

GORDON A. L., D. G. MARTINSON and H. W. TAYLOR (1981) The wind-driven circulation in the Weddell–Enderby Basin. *Deep-Sea Research*, **28**, 151–163.

GROSSI S. M., S. T. KOTTMEIER and C. W. SULLIVAN (1984) Sea ice microbial communities III. Seasonal abundance of microalge and associated bacteria, McMurdo Sound, Antarctica. *Microbial Ecology*, **10**, 231–242.

HOLM-HANSEN O., S. Z. EL-SAYED, G. A. FRANCESCHINI and R. L. CUHEL (1977) Primary production and the factors controlling phytoplankton growth in the Southern Ocean. In: *Adaptations within antarctic ecosystems*, G. A. LLANO, editor, Gulf Publishing Co., Houston, pp. 11–50.

HOPKINS T. L. and J. J. TORRES (in press) The zooplankton community in the vicinity of the ice edge, western Weddell Sea, March, 1986. *Polar Biology*, **8**.

HUSBY D. M. and R. D. MUENCH (1988) Hydrographic observations in the northwestern Weddell Sea marginal ice zone during March 1986. NOAA Technical Memorandum NMFS-SWFC-106, 33 pp.

JENNINGS J. C. Jr, L. I. GORDON and D. M. NELSON (1984) Nutrient depletion indicates high primary productivity in the Weddell Sea. *Nature*, **308**, 51–54.

KAMYKOWSKI D. and S.-J. ZENTARA (1985) Nitrate and silicic acid in the world ocean: patterns and processes. *Marine Ecology Progress Series*, **26**, 47–59.

LEDFORD-HOFFMAN P. A., D. J. DEMASTER and C. A. NITTROUER (1986) Biogenic silica accumulation in the Ross Sea and the importance of Antarctic continental-shelf deposits in the marine silica budget. *Geochimica et Cosmochimica Acta*, **50**, 2099–2110.

MARTIN J. H. and S. E. FITZWATER (1988) Iron deficiency limits phytoplankton growth in the north-east Pacific subarctic. *Nature*, **331**, 341–343.

MIDDLETON J. H. and T. D. FOSTER (1980) Fine structure measurements in a temperature-compensated halocline. *Journal of Geophysical Research*, **85**, 1107–1122.

MUENCH R. D. and J. D. SCHUMACHER (1985) On the Bering Sea ice edge front. *Journal of Geophysical Research*, **90**, 3185–3197.

NELSON D. M. and W. O. SMITH Jr (1986) Phytoplankton bloom dynamics of the western Ross Sea ice-edge. II. Mesoscale cycling of nitrogen and silicon. *Deep-Sea Research*, **33**, 1389–1412.

NELSON D. M. and W. O. SMITH Jr (1987) New and regenerated nitrogen sources utilized by phytoplankton in the ice-edge zone of the Southern Ocean: A comparison between spring and late summer. EOS, **68**, 1708.

NELSON D. M., W. O. SMITH Jr, L. I. GORDON and B. A. HUBER (1987) Spring distributions of density, nutrients and phytoplankton biomass in the ice edge zone of the Weddell–Scotia Sea. *Journal of Geophysical Research*, **92**, 7181–7190.

PAASCHE E. (1973) Silicon and the ecology of marine plankton diatoms. I. *Thalassiosira pseudonana* (*Cyclotella nana*) grown in a chemostat with the silicate as the limiting nutrient. *Marine Biology*, **19**, 117–126.

PAQUETTE R. G., R. H. BOURKE, J. L. NEWTON and W. F. PERDUE (1985) The East Greenland Polar Front in autumn. *Journal of Geophysical Research*, **90**, 4866–4882.

PARSONS T. R., M. TAKAHASHI and B. HARGRAVE (1984) *Biological oceanographic processes*. Pergamon Press, New York, 330 pp.

ROBINSON D. H., J. B. SOOHOO, M. P. LIZOTTE and C. W. SULLIVAN (1987) Detritus is a significant component of the water column particulate material from the Weddell Sea Marginal ice zone in autumn. EOS, **68**, 1765.

SAKSHAUG E. and O. HOLM-HANSEN (1984) Factors governing pelagic production in polar oceans. In: *Lecture notes on coastal and estuarine studies*, O. HOLM-HANSEN, editor, Springer-Verlag, New York, pp. 1–18.

SMITH S. L., W. O. SMITH Jr, L. A. CODISPOTI and D. L. WILSON (1985) Biological observations in the marginal ice zone of the East Greenland Sea. *Journal of Marine Research*, **43**, 693–717.

SMITH W. O. Jr and D. M. NELSON (1985) Phytoplankton bloom produced by a receding ice edge in the Ross Sea: Spatial coherence with the density field. *Science*, **227**, 163–166.

SMITH W. O. Jr and D. M. NELSON (1986) The importance of ice-edge phytoplankton productivity in the southern ocean. *BioScience*, **36**, 251–257.

SMITH W. O. Jr and D. M. NELSON (1987) Primary productivity in the Weddell Sea marginal ice zone: Results from spring and autumn. EOS, **68**, 1708.

SMITH W. O. Jr, M. E. BAUMANN, D. L. WILSON and L. ALETSEE (1987) Phytoplankton biomass and productivity in the marginal ice zone of the Fram Strait during summer 1984. *Journal of Geophysical Research*, **92**, 6777–6786.

SMITH W. O. Jr, N. K. KEENE and J. C. COMISO (in press) Interannual variability in estimated primary productivity of the Antarctic marginal ice zone. In: *Antarctic Ocean and resources variability*, D. SAHRHAGE, editor, Springer-Verlag, Berlin.

SOLORZANO L. (1969) Determination of ammonia in natural waters by the phenolhypochlorite method. *Limnology and Oceanography*, **14**, 799–801.

SOOHOO J. B., S. T. KOTTMEIER, M. P. LIZOTTE and C. W. SULLIVAN (1987) Photoadaptation of phytoplankton and light limitation of photosynthesis at the Weddell Sea ice-edge zone in March, 1987. EOS, **68**, 1708.

STRICKLAND J. D. H. and T. R. PARSONS (1972) A Practical Handbook of Seawater Analysis. *Fisheries Research Board of Canada Bulletin* 167, 2nd edition, pp. 65–70.

WILSON D. L., W. O. SMITH Jr and D. M. NELSON (1986) Phytoplankton bloom dynamics of the western Ross Sea ice edge. I. Primary productivity and species-specific production. *Deep-Sea Research*, **33**, 1375–1387.

ZIMMERMAN R. (1977) Estimation of bacterial number and biomass by epifluorescence microscopy and scanning electron microscopy. In: *Microbial ecology of brackish water environments*, G. RHEINHEIMER, editor, Springer-Verlag, New York, pp. 103–120.

ZWALLY H. J., J. C. COMISO, C. L. PARKINSON, W. J. CAMPBELL, F. D. CARSEY and P. GLOERSEN (1983) Antarctic Sea Ice, 1973–1976: Satellite passive-microwave observations. NASA SP-459, National Aeronautics and Space Administration, Washington, D.C.